DIVING BEHAVIOR, PREDATOR-PREY DYNAMICS, AND MANAGEMENT EFFICACY OF DOUBLE-CRESTED CORMORANTS IN NEW YORK STATE

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DIVING BEHAVIOR, PREDATOR-PREY DYNAMICS, AND MANAGEMENT EFFICACY OF DOUBLE-CRESTED CORMORANTS IN NEW YORK STATE

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The potential for a rapidly growing double-crested cormorant population to negatively impact fish populations and public resources in North America has focused attention on the feeding ecology and management of this federally protected species. Questions persist regarding the nature of cormorant-fish interactions and the propensity for cormorants to impact fish at the population level. From 1998 to 2003, we conducted research and participated in a management program at Oneida Lake, New York, that incorporated nest control and fall hazing to reduce cormorant populations on the lake. We examined: 1) the behavioral response of cormorants to the management program, 2) cormorant prey selectivity, 3) the impact of varying cormorant predation pressures on walleye and yellow perch populations, and 4) daily cormorant activity patterns and underwater foraging habits at Oneida Lake compared to other colonies in New York. I used radio telemetry and weekly counts to reveal that fall hazing moved cormorants off of Oneida Lake, reducing the September population annually by approximately 95% of the 1997 level. Most displaced cormorants relocated to nearby Onondaga Lake rather than leaving the region. Diets examined between 1994 and 2003 consisted of 27 different species, but walleye and yellow perch comprised 58-72% by weight annually. I used the relativized electivity index (E^*) to determine that cormorants selected age 1-3 walleye, and age 2-4 yellow perch, with peak selectivity for age-2 walleye and age-3 yellow perch. A comparison of the electivity values revealed that fish girth (max. circumference) is the main determinant of the maximum size of fish

that cormorants consume. The cormorant control program resulted in a mean reduction in predation pressure on fish populations of approximately 47% from the 1997 level in 1998-2005, which coincided with an increase in abundance of the adult populations of both walleye and yellow perch. Yellow perch survival increased from age-1 to age-3, and walleye survival increased from age-1 to age-4 during this time of predator reduction. Time-depth recorders deployed on cormorants from Oneida Lake, Lake Ontario, and Lake Champlain reveal differences in depth utilization but no disparity in the total time spent diving.

BIOGRAPHICAL SKETCH

Jeremy T. H. Coleman was born in New York, and is a product of the New Jersey public school system. He attended Northern Valley Regional High School at Demarest, and then enrolled at Colgate University in Hamilton, NY, in 1990. In 1992 he was accepted to attend Manchester University in Manchester, England, where he spent a semester studying sociology, archaeology, and the impacts of industrialization on Western culture. Jeremy graduated from Colgate University in 1994 with a B.A. in Anthropology and Sociology, but returned to the realization that his interests lay the study of biology and ecology. In 1995, Jeremy continued his education part-time, taking night and summer classes at Harvard University and Tufts University. During that time, Jeremy worked for the Harvard School of Public Health, where he had his first experience with radio telemetry, studying the movements and roosting locations of passerine birds. He also worked as a veterinary technician at a small animal hospital, and at a wildlife teaching hospital; and as a research assistant for turtle population assessments. Jeremy relocated to Ithaca, NY, in 1997, where he continued his post-baccalaureate education and also worked as a technician on a contraception study for white-tailed deer. In the fall of 1998, Jeremy enrolled in the Department of Natural Resources, at Cornell University, to pursue his M.S. under Dr. Milo E. Richmond, studying foraging movements of double-crested cormorants. Having received a grant from the USFWS Wildlife and Sport Fish Restoration Program in 2001, he continued with his doctoral research at Cornell University, extending and initiating analyses of cormorant interactions with fish, foraging behavior, and the effects of management practices. Jeremy Coleman is currently employed as an endangered species biologist with the U.S. Fish and Wildlife Service in Cortland, NY, and he lives in Syracuse with his wife, Emily, and his two girls, Juliet and Ginger.

This work is dedicated to my family, for their love, support, and patience;

and especially to Juliet, my reason to smile every day.

The bird thinks it is an act of kindness to give the fish a lift in the air.

- Sir Rabindranath Tagore

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CHAPTER 1:

AN INTRODUCTION TO CORMORANT MANAGEMENT AND CURRENT RESEARCH IN CENTRAL NEW YORK

Contemporary wildlife management has evolved in recent years, reflecting changes in the types of interactions between people and wildlife, and an increasing involvement of stakeholders in decision-making (Decker et al. 1996; Decker and Chase 1997). Current management theory espouses the increasing integration of sociological and biological dimensions, and emphasizes the role of informed citizens in identifying management objectives based on human values, perceptions, and desired impacts (Chase et al. 2001; Riley et al. 2003). The adaptive implementation of management actions to achieve fundamental objectives established by stakeholders, known as Adaptive Impact Management (Riley et al. 2003), has been proposed as a preferred method for increasing stakeholder investment and satisfaction in wildlife management, while maintaining a dynamic program that facilitates experimentation and learning opportunities for both professionals and the public (Enck et al. 2006; Riley et al. 2002, 2003). Integral to the success of this process is the receptiveness of a management agency to the input of citizen stakeholders, and an appropriate forum for the exchange of ideas by various stakeholder groups. Faced with strong public beliefs that a growing double-crested cormorant (*Phalacrocorax auritus*) population in upstate New York was detrimental to sport fishing and island habitats in two of the state's premier fisheries, the New York State Department of Environmental Conservation (NYSDEC) pursued an adaptive impact management approach in 1994 by first convening a citizen's task group, and later a search conference, to develop management objectives for Oneida Lake and eastern Lake Ontario (Miller 1998;

Schusler and Decker 2002). It was evident at that time that double-crested cormorants (cormorants) had begun to exceed public wildlife acceptance capacity (Decker and Purdy 1988) in the region, but concern within the agency over competition for nesting space between cormorants, gulls, and the state-listed common tern (*Sterna hirundo*) was also a catalyst for management action.

The cormorant population was relatively small in North America through the first quarter of the 20th Century, estimated at 27,000 breeding pairs, ca. 1928 (Lewis 1929). The gradual population increases observed from the 1920s through the 1940s were reversed in the 1950s - 1970s, when cormorants suffered from the same organochlorine pesticides that impacted many other predatory bird species (reviewed by Wires and Cuthbert 2006). In the last ¼ of the 20th Century, cormorant numbers increased rapidly throughout much of North America, rising to approximately 270,000 breeding pairs for the interior population alone (Wires and Cuthbert 2006), and exceeding all population estimates previously recorded (Hatch and Weseloh 1999). Wires and Cuthbert (2006) estimate the breeding population to In the Great Lakes, breeding cormorant populations increased an average of 28.8% annually between 1970 and 1991, then slowed to an average 15% annual increase from 1991 to 2000 (Weseloh et al. 2002; Wires et al. 2001). Several factors are credited for their success, including a reduction of contaminants in the environment, particularly DDT and its metabolites, and an increase in food resources, especially the growth of the aquaculture industry in the southeastern U.S. and increases in forage fish in the Great Lakes (reviewed by Wires and Cuthbert 2006). Protection from human persecution, chiefly afforded through the Migratory Bird Treaty Act of 1972, furthered the birds rapid population recovery.

A cormorant colony established in 1974 on Little Galloo Island, in the eastern basin of Lake Ontario (Weseloh and Ewins 1994), preceded the initiation of cormorant

nesting on Oneida Lake, New York, by 10 years (Claypoole 1988). Transient cormorants were observed on Oneida Lake in the late 1970s and early 1980s, but numbers remained low (S. R. Severinghaus, Cornell Biological Field Station (CBFS), unpublished data; J. L. Forney, CBFS, personal communication). Breeding populations grew throughout the region in the '80s and '90s, resulting in annual increases in the number of resident and migrating cormorants using Oneida Lake in late summer and autumn, during the migration period (see Coleman 2003, Chapt. 1, for the history of recorded cormorant observations in central New York). Declines in walleye (*Sander vitreus*) and yellow perch (*Perca flavescens*) populations through the 1990s in Oneida Lake, also corresponded with the increasing presence of cormorants (VanDeValk et al. 2002; Rudstam et al. 2004), as did reductions in the nesting space available to other colonial bird species breeding on the lake. These observations tempered public opinion and increased political pressure, ultimately resulting in a two-part adaptive management plan, instituted by NYSDEC from 1998 to 2003 to both: 1) reduce the predation impact on fish by reducing the number of resident and migrant cormorants on the lake in the fall through a novel harassment/hazing regimen (Chipman et al. 2000), and 2) limit through nest control the impacts of resident cormorants on nesting habitat on the lake, and thus on the other resident colonial waterbird species (Miller 1998). Starting in 2004 this program was expanded to prevent all cormorant reproduction on Oneida Lake and further reduce cormorant consumptive impacts through a season-long hazing regimen (NYSDEC 2004).

The rapid growth of the cormorant population on Oneida Lake, followed by subsequent metered declines in consumptive pressure resulting from the management programs provided the opportunity to examine food-web interactions in the large lake through the manipulation of predator abundance. Such manipulations constitute a type of "press" perturbation experiment (Bender et al. 1984), and present an opportunity for

learning (Carpenter 1990). The fish population data available for Oneida Lake, specifically for percids (walleye and yellow perch), span 50 years, and provide an excellent baseline for a natural experiment. The history of research and monitoring of the cormorant population on Oneida Lake also extends back to the inception of the colony in 1984, and cormorant diet has likewise been studied since 1988. A robust diet study was initiated in 1994 and was continued annually through 2003, after which the prevention of all chick production, as per the augmented management program, precluded the collection of the regurgitated diet samples that had constituted the majority of the samples collected starting in 1998.

There are 3 main topics that pervade the following chapters of this dissertation: 1) cormorant diet and potential impact to fish populations, 2) the behavioral and numerical response of cormorants and fish populations to the adaptive management program, and 3) the foraging behavior and diving ability of wild double-crested cormorants. While these topics are interspersed among the different chapters, the 2nd and 3rd chapters focus mainly on responses to management, and the 4th and 5th chapters are concerned with cormorant foraging behavior and diving capability.

The objectives of Chapter 2 are: 1) to document the numerical growth of a founder population of double-crested cormorants, originating in 1984 on Oneida Lake, and 2) to detail the immediate and ultimate behavioral response of cormorants to non-lethal management practices and egg-oiling during the first 6 years of a management program, initiated in 1998. The cormorant colony on Oneida Lake exhibited an average annual growth of 35% between 1988 and 1998, commensurate with growth rates from some Great Lakes colonies in the 1980s (Weseloh et al. 2002). We found that average annual colony growth dropped between 1998 and 2003 ($\overline{x}$ = -1.7%), but high water events in the spring of 2000 and 2002, which flooded the islands, likely contributed to the annual declines. We tracked local movements of cormorants in the

fall using radio telemetry and a standardized point counting technique at several local water bodies. Coincident with the initiation of annual hazing, most cormorants left Oneida Lake, but the majority appeared to relocate to Onondaga Lake, approximately 20 km to the southwest of Oneida Lake. Juvenile cormorants radio tagged in 2003 responded to hazing as the adults had, and many also moved to Onondaga Lake rather than emigrating from the region.

Chapter 3 focuses chiefly on the trophic interactions between cormorants and fish in Oneida Lake, and on the effect of reduced cormorant predation pressure on fish populations. The objectives of the chapter are: 1) to elucidate the age-specific impact of cormorants on percids, 2) to revisit the status of walleye and yellow perch populations in Oneida Lake following the first 8 years of an ongoing cormorant management program, 3) to re-analyze recruitment dynamics for walleye and yellow perch to examine the effects of reduced cormorant predation on recruitment of adult fish, and 4) to discuss percid population trends over a 20 year period (mid-1980s to 2005) given the current understanding of cormorant-fish interactions. Cormorant diet was examined annually from 1994 to 2003, and the samples examined for this project (n = 2375 regurgitated boluses, n = 137 stomach samples) included specimens from 27 different species, and consisted of 58-72% walleye and yellow perch by weight annually. The availability of abundance estimates of all age classes of these two species allows for calculations of selectivity of cormorants to different age classes using the relativized electivity index (E^*, Vanderploeg and Scavia 1979). Cormorants generally selected age 1-3 walleye, and age 2-4 yellow perch, with peak selectivity for age-2 walleye and age-3 yellow perch. The peaks of the electivity curves align when plotted against fish girth (max. circumference), but not when plotted against fish total length, which suggests that fish girth is the main determinant of maximum size of fish that cormorants will consume. The cormorant control program resulted in a mean

reduction in predation pressure on fish populations of approximately 47% from the 1997 level (range: 30-83%) in 1998-2005. The reduction in cormorant feeding days coincided with an increase in abundance of the adult populations of both the walleye and yellow perch. For walleye, this also coincided with an increase in survival from age 1 to age 4, although this increase is larger than expected from the level of cormorant reduction alone. Other factors, such as an increase in gizzard shad and white perch since 1997, which provide an alternate prey for cormorants, may have contributed to lower cormorant predation on walleye. Alternatively, recruitment of walleye to age 1 could have been larger than was revealed in our trawl samples, also possibly in response to increases in gizzard shad. The increase of yellow perch survival from age 1 to age 3 was not as large, but was consistent with our expectations. Although the observed increase in adult populations of both percid species is consistent with expectations following cormorant control, the magnitude of the increase in walleye was larger than expected based on the degree of decline in cormorant feeding days.

The objectives of Chapter 4 are: 1) to determine the times of day that radio-tagged cormorants were away from a colony site on a temperate freshwater lake in New York, and 2) to examine how daily foraging patterns change through the breeding season. I found that radio tagged cormorants had a bimodal daily activity pattern on Oneida Lake in July, 2000. Cormorants were most likely to be off the island at 09:00 and 15:00 Eastern daylight time. The pattern of activity appeared to change slightly in August, with a shift from a less synchronous pattern of departures to a greater focus on morning activity also centered around 09:30. These results correspond with daily observations of great cormorant (*P. carbo*) foraging activities reported for colonies in Africa and Poland.

Lastly, in Chapter 5, I report on a study designed to: 1) characterize the diving abilities and underwater foraging habits of double-crested cormorants at their breeding grounds in the northeastern U.S., and 2) to compare foraging effort in 3 large lakes, each with different bathymetric profiles and different assemblages of fishes constituting the respective prey base. I deployed time-depth recorders (TDRs) on breeding age cormorants at colonies on Oneida Lake, Lake Ontario, and Lake Champlain, and monitored diving behavior of individuals over several days. This study is the first to use TDRs to examine the diving behavior of free-ranging double-crested cormorants. The dive data reveal differences in depth utilization by lake, likely attributable to differing prey species, but no disparity in the total time spent diving. The maximum depth recorded was 25.8 m, collected at Lake Ontario. Mean dive depths for individual birds ranged from 1.6 m to 10.6.

RECOMMENDATIONS

The results presented in these chapters illuminate some clear needs for further research. Aquatic systems can harbor very complex trophic interactions, where indirect impacts and compensatory mechanisms can obscure the key drivers of community dynamics. Moreover, our ability to collect the best information to elucidate these interactions can be biased and/or compromised. Understanding the limits of sampling methodology and the errors inherent in different techniques is a good start to accommodating these issues, but it will be through computer modeling and simulation that we may best be able to gain improved insight into these complex systemic interactions. The long-term data available for Oneida Lake yellow perch and walleye populations (>50 yrs) are possibly the most comprehensive in North America, and yet there are challenges to conclusively drawing inference on causative relationships from the historic trends and events captured in this record. The

development of age-structured estimation models (see Irwin et al. 2008) helps to smooth out irregularities in population estimates from sampling variability, providing more consistent estimates and increasing predictive confidence. Simulation modeling, using either improved estimates or conventionally derived numbers, can be an effective tool for exploring indirect interactions that might not otherwise be apparent. These approaches, which are gaining in sophistication with computational advances, may be the best tools for studying complex predator-prey interactions at the population level, and elucidating the role of cormorants in aquatic food webs.

Due to the temporal and spatial variability in fish species composition and cormorant diet, the potential for cormorants to impact valuable fish species is site specific. Results of diet analyses from Oneida Lake and elsewhere demonstrate the importance of monitoring cormorant diet at sensitive locations if negative impacts are suspected. At Oneida Lake, I found that prey selectivity within species is based on size, and cormorants essentially selected the largest fish (perch or walleye) they could swallow. This strategy agrees with the tenets of optimal foraging theory (Emlen 1966, MacArthur and Pianka 1966), whereby consumption of larger fish maximizes caloric intake per unit time. However, optimal foraging concerns may also support the shift to gizzard shad (*Dorosoma cepedianum*) that we observed in late summer and fall in years of high shad abundance. Despite their small size, gizzard shad have a high caloric content, and their schooling behavior might make them easier to catch, particularly by cormorants employing social (flock) foraging texhniques. Coleman et al. (in review) also observed a dietary shift towards schooling "forage" fish, namely gizzard shad and emerald shiner (*Notropis atherinoides*), by cormorants foraging in the Niagara River in years when they were abundant, and Johnson et al. (2003) also noted a similar shift to alewife (*Alosa pseudoharengus*) in Lake Ontario which coincided with annual spawning migration to the nearshore. Differential species

selection by foraging cormorants raises a number of questions that warrant further examination. Whatever the driving factors, however, the flexibility that cormorants demonstrate necessitates that dietary analyses be initiated or continued at any and all sensitive locations where deleterious effects of cormorant predation are suspected.

Lastly, there continues to be a critical need for the advancement of the social component of cormorant management in North America. For the reasons discussed above, and also in Chapter 3, the determination of a fixed number or density of cormorants that will be biologically sustainable may be difficult given the potential for considerable regional variability. However, defining a population level that is socially acceptable may be an even more important, yet elusive task The idea that cormorant populations have exceeded a public acceptance threshold is generally recognized, however, there has been little progress in defining that threshold and determining how such information, or some such socially derived criterion, might be used to establish management objectives. One of the main criticisms of current cormorant management is that the target population size(s) and justification are not clear, and that is a cause of consternation for many. Continued and/or renewed efforts to bridge the gap between biological and social concerns will be critical for the success of cormorant management in North America in the immediate future.

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CHAPTER 2:

NUMERICAL AND BEHAVIORAL RESPONSE OF DOUBLE-CRESTED CORMORANTS TO NEST MANAGEMENT AND HAZING, 1998-2003

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Abstract.- Management of double-crested cormorants to protect public natural resources has moved from conjecture in the 1990s to policy in the Great Lakes region of the U.S. since the finalization of a public resource depredation order in 2003. Previously, piscivorous bird control had generally been relegated to aquaculture facilities in the southeastern U.S. where the direct link between cormorant presence and palpable economic loss was more obvious. In the mid-1990s, however, concern over double-crested cormorant predation impacts to recreational fisheries, and interspecific competition for nesting space between local waterbird species, resulted in the implementation of an intensive management program on Oneida Lake, New York. Management plans were designed and implemented to reduce reproductive success and fall migrant populations through 1) nest management, allowing only 100 successful nests per year and 2) a non-lethal lakewide hazing program. In conjunction with other waterbird research, we collaborated to monitor the results of this program for 6 years (1998-2003) through weekly counts of nests and adults on the lake, and through studies tracking the movement of adults and juveniles around the Oneida Lake region. Egg oiling and nest removal effectively reduced annual reproductive success of target nests by approximately 99%, and ultimately reduced the rate of growth for the colony, which changed from an average annual growth of 35% between 1988 and 1998, to an average of -1.7% from 1998 to 2003. Impacts of high water in 2000 and 2002, which flooded the nesting island, likely contributed to declines in colony growth rate as well. Hazing techniques, implemented by USDA-Wildlife Services personnel, integrated proven methods from the aquaculture industry and new approaches conceived for this effort. Hazing successfully moved cormorants off of Oneida Lake in late summer, consistently reducing the September population by approximately 95% of the 1997 level. Radio-tagged juvenile cormorants responded to hazing

similarly to tagged adults, with most relocating to Onondaga Lake, 20 km from Oneida Lake, rather than emigrating from the region.

Key words.- adaptive management, cormorant, egg oiling, Great Lakes, harassment, hazing, impact, nest control, non-lethal, Oneida Lake, *Phalacrocorax auritus*, radio telemetry

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The rapid growth of double-crested cormorant populations throughout much of North America in the past thirty years (Hatch 1995; Tyson et al. 1999; Weseloh et al. 1995, 2002) has become a source of concern for aquaculturists, anglers, and fisheries, wildlife, and habitat managers throughout their range, not just in New York (Glahn and Brugger 1995; Trapp et al. 1999; Glahn et al. 2000; Wires et al. 2001; Hebert et al. 2005). Of major concern is the potential negative impact of cormorants on sport fish and aquaculture resources (Trapp et al. 1999; Suter 2000; USDI/FWS 2003; Wires et al. 2001, 2003). In New York the number of double-crested cormorants using Oneida Lake increased annually starting in the late 1970s (Cornell Biological Field Station, unpublished data). The first nest was reported in 1984 (Claypoole 1988), and nesting expanded through the ‘80s and ‘90s. Coincident with the expanding breeding population were annual increases in the number of cormorants foraging on Oneida Lake in late summer and autumn during their migration from nesting sites in the lower Great Lakes and the St. Lawrence River to southern overwintering areas. Declines in walleye (*Sander vitreus*) and yellow perch (*Perca flavescens*) populations through the 1990's, also corresponded with the increasing presence of double-crested cormorants on the lake (VanDeValk et al. 2002; Rudstam et al. 2004), as did reductions in the nesting space available to other colonial bird

species breeding on the lake. In 1998 a two-part adaptive management plan was enacted by NYSDEC to both: 1) reduce the predation impact on fish by reducing the number of resident and migrant double-crested cormorants (hereafter cormorants) on the lake in the fall through a novel harassment/hazing regimen, and 2) limit the spatial impacts of resident cormorants on nesting habitat through nest control procedures. This pioneering effort, initiated by New York State Department of Environmental Conservation (NYSDEC) and enacted by United States Department of Agriculture-Animal and Plant Health Inspection Service - Wildlife Services (APHIS-Wildlife Services) and New York Cooperative Fish and Wildlife Unit (NYCFWRU) at Cornell University, resulted from recommendations made by the citizen's task group to minimize cormorant predation pressure on walleye and yellow perch (Chipman et al. 1998), and from the goals established by NYSDEC for maintaining the diversity of colonial waterbirds breeding on Oneida Lake, with an emphasis on enhancing the common tern population. The objectives of this program were maintained for 6 seasons, 1998 through 2003, before being expanded in 2004 to further reduce potential cormorant impacts through a more aggressive full-season management regimen (NYSDEC 2004). A telemetry study conducted in 1999 and 2000 to examine cormorant foraging movements and behavior during the breeding season on Oneida Lake (Coleman et al. 2005) also provided the means to investigate ways in which the fall hazing program affected daily cormorant movements and the destination of displaced cormorants.

The objectives of this paper are: to document the numerical growth of a founder population of double-crested cormorants, originating in 1984 on Oneida Lake, New York, and to detail the immediate and ultimate behavioral response of cormorants to various management practices during the first 6 seasons of a management program (initiated in 1998). To address the latter objective, we asked the

following questions: 1) what are the effects of continued nest control and post-breeding hazing on annual cormorant breeding effort at the colony level; 2) what is the proximate response of cormorants to a non-lethal adaptive hazing program designed to move resident and migrating cormorants off of a large temperate lake during late summer/fall; and 3) how do juvenile cormorants respond to late-summer hazing at their natal colony relative to the response of breeding-age adults at the same location? Given the proximity of Oneida Lake to large cormorant colonies on Lake Ontario, and the rapid expansion of Oneida Lake's resident population commensurate with the other large colonies in the Lake Ontario basin, Oneida Lake is an excellent model for many of the inland lakes in the Great Lakes region of North America that have experienced similar cormorant population growth in the past 20 years.

METHODS

Study Area and Existing Conditions

This study incorporates count data collected over 20 seasons (1984-2003), and more intensive studies corresponding with a management period of 6 years (1998-2003) on and around Oneida Lake, New York. Oneida is a large shallow lake, with a surface area of 207 km^2, a maximum depth of 16.8 m, and an average depth of 6.8 m. Walleye have been stocked in Oneida Lake since 1893, and the lake supports one of the most valuable sport fisheries in the state (Connelly and Brown 1991). Comprehensive long-term fisheries data available for Oneida Lake, extending back to 1956, provide an excellent foundation for the study of cormorant-fish interactions in this system. Walleye and yellow perch are the most numerous fish in the lake, and, with the exception of 1999, account for 55-93% of all fish caught annually in gill net surveys since 1958 (VanDeValk et al. 2004), and 58-77% of annual cormorant diet by

weight on Oneida Lake since 1988 (VanDeValk et al. 2002; Rudstam et al. 2004; Coleman 2009, Chapt. 3).

From a single pair of cormorants in 1984 (Claypoole 1988), the Oneida Lake colony grew rapidly to a maximum of 365 pairs by 2000 (Coleman et al. 2005). Three small islands in the northwest region of Oneida Lake provided nesting habitat for colonial waterbirds, two of which, Wantry Island (43°13.48'N, 076°00.08'W) and Long Island (43°14.70'N, 076°00.05'W), have been used by cormorants. In recognition of an initial concern to limit the cormorant population using Long Island, biologists with NYCFWRU and NYSDEC, operating under federal depredation permit, repeatedly removed all cormorant nests from that island from 1991 to 1993, and the effects on re-nesting effort were studied (R. Pooler, Cornell Biological Field Station, unpublished report). These initial actions prevented colonization of Long Island by cormorants, thereby maintaining nesting habitat for the common tern and other bird species. From 1994 to 1997, cormorants were allowed to nest unrestricted on the lake to facilitate studies of cormorant/fish and cormorant/tern interactions. Faced with an expanding cormorant population, cormorants were again allowed to nest on Long Island starting in 1998, but nesting was prevented elsewhere on the lake.

Population Estimates

Oneida Lake.--

There are three main groups that comprise the summer population of cormorants on Oneida Lake: 1) breeding adults that arrive in early spring, 2) juveniles reared on the lake, and 3) non-resident migrants that inhabit the lake beginning in mid/late July. Non-breeders and sub-adult cormorants have not been prevalent at this colony during peak nesting from April – June (unpublished data). Biologists with Cornell University and the NYCFWRU counted cormorant nests annually on Oneida Lake, starting with the first nest in 1984 (**Table 2.1**). From 1995-2003 adult

cormorants were counted weekly, often multiple times per week, to monitor the influx of migrants to Oneida Lake. We censused cormorants by boat using binoculars, at a distance of 75-150 m from the roost, and counted birds at least 3 times to derive an average for each location. Most counts were made at dusk, when cormorants were roosting, or at dawn before birds left their roosting sites (Coleman and Richmond 2007, Coleman 2009, Chapt. 4). Counts were conducted at all known historic loafing and roosting sites on the lake, and provide a lake-wide census of the population. During the hazing period, counts were conducted similarly on Sunday evenings following a 2-day respite from hazing activities which began Monday morning and continued through Friday afternoon (see below).

Regional.--

To monitor late-summer and fall cormorant movements throughout the region, we conducted fall surveys of six additional large water bodies within 55 km of Oneida Lake starting the second week of August and continuing through September, 1998-2000. We devised two separate travel routes, each providing thorough coverage of 3 distinct water bodies, and established 3 to 5 viewing locations along the shoreline of each of the 6 water bodies. Viewing locations were at least 0.4 km apart, and were selected based on lake surface visibility and ease of access. One route encompassed Cross, Otisco, and Skaneateles lakes; the other included Onondaga and Cazenovia lakes, and a 20 km section of the Oneida River from the outlet of Oneida Lake to its confluence with the Seneca and Oswego rivers (43°12.08'N, 076°16.74'W). Surveys were conducted 4 days per week, weather permitting, and the 2 routes were alternated. Each water body was surveyed twice weekly, with starting times varying between 0700 and 1300 hrs, thereby alternating count times at each site between morning and afternoon. Counts were conducted using a standardized 3-minute time-area sampling regimen, during which all birds visible to the naked eye were recorded. Binoculars

and spotting scopes were used to verify species. The total number of cormorants observed at each water body was then recorded for each visit.

Radio Telemetry

Radio tracking.--

We used radio telemetry to track the movements of breeding adults and fledged juveniles over three different nesting seasons. In 1999 and 2000, we radio-tagged 15 adult double-crested cormorants each year on Oneida Lake (for complete methods see Coleman et al. 2005), and in July 2003 we tagged an additional 8 fledged juveniles on the nesting island. Radio transmitters weighed approximately 28 g (< 2% body weight), transmitted 55 beats/min between the frequencies of 172.010 and 173.995 MHz, and were equipped with mortality indicators (ATS, Isanti, Minnesota). We deployed 35 radio tags backpack style using a ribbon harness (Dunstan 1972; King et al. 2000), and another 3 in 1999 with 19 mm waterproof tape (Wanless et al. 1999; Quintana 2001). The tape method failed and all 3 tags were recovered within two weeks. We banded all cormorants with Federal aluminum bands and used coded color markers to enable visual identification of individuals: yellow patagial tags for adults and blue plastic leg bands for juveniles.

We tracked adult cormorants during daylight hours from early July through September using programmable ATS model R2000 receivers. Each season, prior to the start of hazing, we relocated radio-tagged cormorants by 1) homing-in on transmitters by boat, 2) triangulation from 2 points on shore, or 3) aerial tracking by airplane. The location of birds found by homing-in was recorded using a hand-held GPS unit with a horizontal accuracy of 5 to 15 m. Location by triangulation was accomplished by establishing 4 receiving stations along the south shore of the lake. The effective range of signal detection at the two main stations, the Cornell Biological Field Station (CBFS) at Shackelton Point (43°10.58'N, 075°55.98'W) and Valentines

Beach (43°12.71'N, 076°02.08'W), was approximately 10 km and 7.5 km, respectively. The two additional south-shore locations were used to bring tags into range and to achieve an optimal alignment between the transmitter and receivers (White 1985; White and Garrot 1990). Hand-held VHF radios allowed us to coordinate simultaneous signal reception. Two fixed transmitters, positioned on Long Island and Wantry Island, allowed for error estimation in daily receptions.

During the active hazing period, namely September 1999 and 2000, adult cormorants were located through 1) homing-in by boat, 2) aerial tracking, or 3) from a single vector and visual estimation during road surveys of regional water bodies. Flights for aerial tracking were conducted once prior to hazing (late August) in both years, then twice in September 1999 and three times in September 2000. Aerial tracking was conducted at an altitude of 2000-2500 ft. (~610-760 m), using a 3-element Yagi antenna to determine cormorant location based on signal strength and clarity. Dummy transmitters at fixed locations were used for reference. Radio-tagged juvenile cormorants were located through homing-in and by single vector estimation during the hazing period in 2003.

Vector data collected during triangulation were plotted using Location of a Signal software (v.2.01, Ecological Software Solutions, Sacramento, California). We imported the bearing intersect points into ArcView GIS (v.3.3, ESRI, Inc., Redlands, California) for qualitative spatial analysis, and added the coordinates for locations collected through homing. Animal Movement Analyst Extension (AMAE) to ArcView was used to generate kernel utilization distribution contours (Hooge and Eichenlaub 1997). Animal Movement Analyst Extension employs a fixed kernel method to estimate home range, and we selected Least Squares Cross Validation (after Silverman 1986) to determine smoothing parameters (Seaman and Powell 1996). We generated the smoothing factor for all point data combined (h = 1748), and used it

separately for both pre-hazing and hazing estimates. Kernel estimates of density can be interpreted as approximations of utilization distribution (UD) (Seaman et al. 1999), which represent a two-dimensional relative frequency distribution of animal locations over time (Van Winkle 1975). We generated isopleths from adult cormorant locations depicting UDs by probability (e.g. 50%, 75%, and 90%), to compare distributions before and after hazing.

Automated receiver.--

We used an automated receiving station on Long Island (ATS model R2100 receiver and model D5041 data collection computer) to record the daily presence of radio tagged cormorants on the nesting island in 2000 and 2003. In both years, the receiver and logger were housed in a strongbox at the center of the nesting area (see Coleman and Richmond 2007), powered by a 12 volt marine battery and maintained by a photovoltaic panel (Solarex model MSX-10L, Frederick, Maryland). An omni-directional dipole antenna (Cushcraft Corp. model CRS-150, Manchester, New Hampshire), was erected and extended approximately 2.5 m above the surface of the island. To filter extraneous signals, the receiver was programmed to scan each frequency for 30 seconds every half-hour, and to record only transmissions within a small range of rates, approximately 53-57 beats per min. A fixed transmitter, positioned on Long Island, verified daily logger function. The date, time, and transmission rate of each accepted signal was logged, then downloaded to a laptop computer during weekly trips to the island. Downloading required approximately 15 min, occurred at varying times during daylight hours, and caused minimal disturbance to the colony. During the weeks prior to hazing, the sensitivity (gain) of the receiver was tuned to detect transmitters located on the entire island, a range of approximately 200 m. Once hazing began, the range was expanded to exceed 1500 m in hopes of detecting tagged cormorants on or near any of the small islands in the northwestern

part of the lake. For this study, we focused on cormorant location and movement during the 3-4 weeks before and after the initiation of the hazing program, which includes August through September.

Management Actions

Nest Control.--

In 1998, a target population objective of 100 nesting pairs of cormorants was established by NYSDEC biologists and cooperators to maintain a viable community of colonial waterbirds on Oneida Lake. To achieve this target objective, we enacted a nest control program consisting of: weekly egg and nest removal (1998-1999), construction of experimental exclusion barriers (1999), and weekly egg oiling using food-grade corn oil (2000-2003) (Gross 1951, Bédard et al. 1995, Shonk et al. 2004). Cormorants were restricted to nesting solely on Long Island, so all nests initiated at other locations were removed. Over the 6 years of this program, 1998-2003, the eggs in 100 nests were allowed to develop undisturbed each year, and the fates of all nests were monitored. All nest management actions were conducted by NYCFWRU personnel, in compliance with state and federal depredation permits and animal care and handling protocols (Federal Depredation Permit MB769046-0; Protocol # 01-91).

Fall hazing.--

All official hazing activities were conducted by APHIS-Wildlife Services personnel. Techniques used to frighten cormorants were similar to those used successfully in the southeastern United States to disperse wintering cormorants from ponds and night roosts near aquaculture facilities (Mott and Boyd 1995; Mott et al. 1998; Reinhold and Sloan 1999; Tobin et al. 2002; Barras and Godwin 2005). To counteract habituation of cormorants to the methodology, the hazing program was adaptive in application, and included various combinations of tactics during the hazing period. Active techniques included pursuit of birds by boat and the use of pyrotechnic

noise-makers to disrupt flocks of birds wherever they were found. Static scaring devices were employed at common loafing and roosting islands and shoals, including Long Island and Wantry Island, where cormorants frequently nested and loafed. Static devices included propane exploders, inflatable human effigies, electronic sirens, predator eye balloons, and red and silver Mylar® tape strung between fence posts around the shoreline or perimeter of a loafing area (Chipman et al. 1998, 2000). Because the common tern is listed as a threatened species in New York, care was taken to avoid negative impacts to terns (see Mattison 2006). No active harassment was conducted within approx. 300 m of the terns' primary nesting location on Little Island, and no fixed devices were installed on Little Island. A separate manuscript detailing hazing methodology and the efficacy of specific techniques is currently in preparation (J. D. Taylor, APHIS-Wildlife Services, personal communication).

From 1998-2002, the fall hazing program was conducted annually during the month of September, with start dates ranging from 1-5 September. In 2003, with concurrence of NYSDEC, the start date was advanced two weeks to 19 August. During these six years, hazing activities were conducted approximately from dawn to dusk, weather permitting, during weekdays only. Active hazing and use of loud static devices like propane exploders, were not conducted on weekends to avoid conflicts with recreational use of the lake (Chipman et al. 1998). The hazing program was terminated by 1 October each year to avoid overlap with opening of the waterfowl hunting season.

RESULTS

Breeding Population

Between 1988 and 1998 the breeding population of cormorants on Oneida Lake increased from 30 to 332 pairs of birds, representing an average annual increase

of 35% (Table 2.1). From 1998 through 2003, nest control reduced the annual number of nests to fledge at least one chick to approximately 100 ($\overline{x}$ = 96.2, SE = 15.3), with an annual mean number of fledged chicks = 157.5 (SE = 27.1). Egg oiling in 2000 to 2003 prevented hatching in approximately 99% of nests treated, consistent with previous accounts (Bédard et al. 1995). Starting in 1999, the first season after the nest control plan was enacted, annual population growth rate declined drastically from 23% (1997 to 1998) to 2%, an increase of just 7 nests. The rate of growth in 2000 was likewise low at 8%, and this was the year in which we recorded 365 nests on Long Island, the largest number of simultaneously active nests recorded for the Oneida Lake colony. High water events in May of 2000 and 2002 flooded the nesting islands after the peak number of active nests was recorded in each year, and post-flood peak nest counts declined by 33% (365 to 244 nests in 2000) and 26% (300 to 222 nests in 2002).

Annual Population Chronology and Hazing

Breeding adult cormorants, fledged chicks, and non-nesting migrants repeatedly displayed a unique annual pattern of arrival and departure on Oneida Lake during this study (Fig. 2.1). Adult cormorants were present by early April, occasionally before ice-out, with nest construction beginning in mid-April. The first eggs were laid by the last week of April. Numbers of adult cormorants increased through mid May to between 500 and 800 birds, with the number of active nests peaking in late May or early June. As chicks reached adult size and fledged in late June, they were included in the counts of adult (adult-sized) cormorants. Non-resident migrants began to appear on Oneida Lake during the third week in July each year, and the number of cormorants on the lake would increase rapidly thereafter. Prior to the fall hazing program, numbers of cormorants increased steadily through August and into late September, reaching almost 2700 birds in 1996 and 1997 (Table 2.1).

Migrant and resident cormorants remained on Oneida Lake in large numbers until the second week of October, when numbers would decline sharply coincident with the opening of the waterfowl hunting season (14, 12, and 11 October from 1995-1997, respectively). Fall departures were frequently offset by apparent new arrivals, so actual counts in late September and October fluctuated considerably.

Coincident with APHIS-Wildlife Services hazing activities, our September counts of cormorants revealed a substantial reduction in the number of adult-sized birds on Oneida Lake compared to values collected in the mid-1990s (Fig. 2.1). Peak counts immediately prior to hazing ranged from 1114 to 1964 cormorants; the variation due likely to annual differences in weather patterns affecting the timing of migrational movements, and not to nest control efforts or inter-annual effects of the hazing program (J. Coleman, personal observation). The year 2003 was unusual in that hazing was initiated 2 weeks earlier than in previous years (19 August), and, while having the same immediate effect of driving birds off the lake, was preceded by a decline of over a quarter of the population (~350 birds) during the week before hazing began. A contributing factor that likely impacted this movement of cormorants off of the lake in early August, 2003, was the active collection of cormorants to monitor an outbreak of cormorant Newcastle virus, first observed on Oneida Lake that season (Coleman et al. 2003, National Wildlife Health Center 2003). Over several days, personnel with the New York State Wildlife Pathology Unit repeatedly visited the nesting island to collect symptomatic cormorants. Approximately 30 hatch-year cormorants were affected and/or collected at that time, several of which were shot from a boat using a 12 gauge shotgun. These activities may have resulted in disturbances at the nesting island akin to hazing, but preceding the official initiation of the program on 19 August.

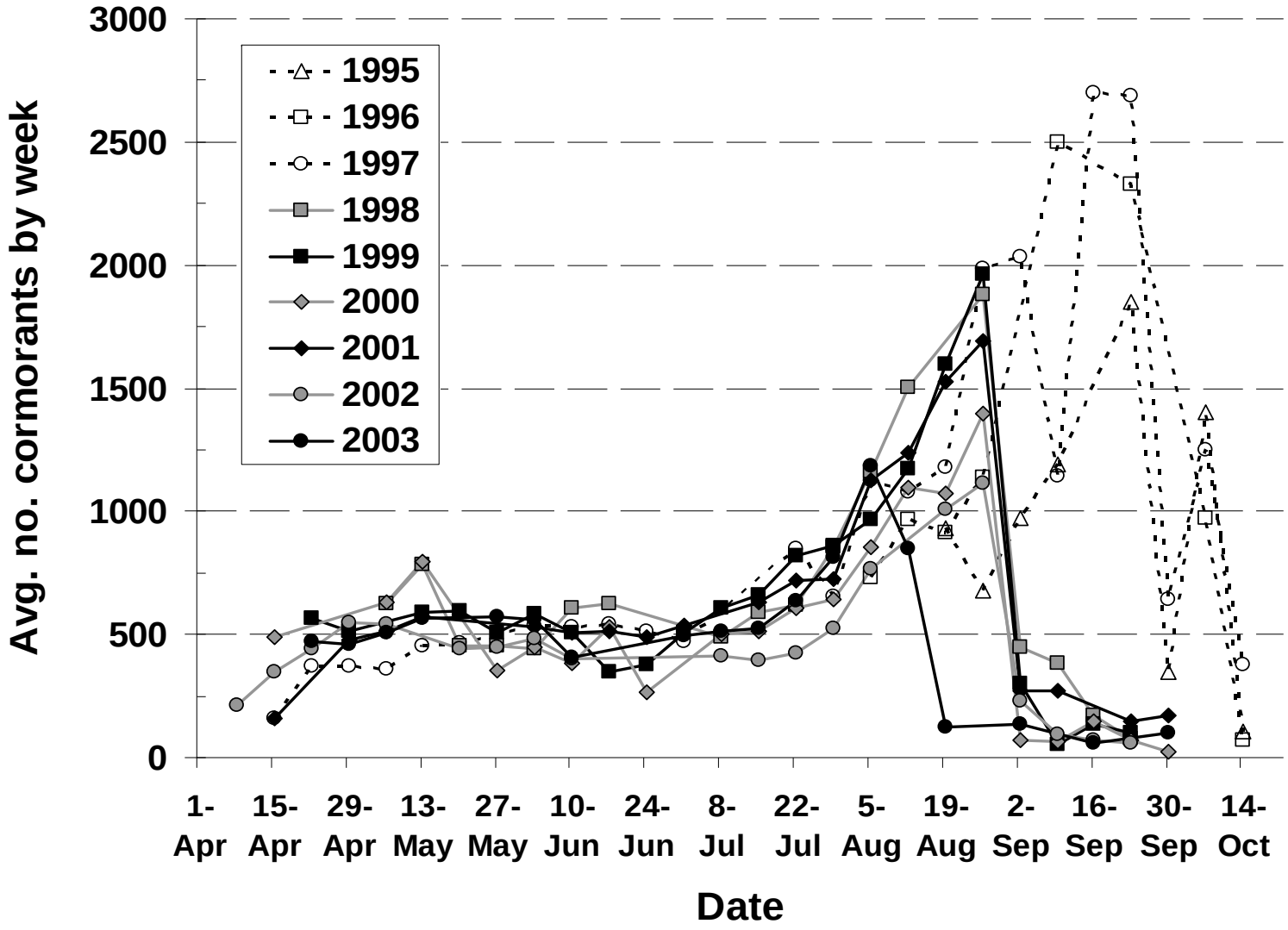
Table 2.1. History of the double-crested cormorant nesting effort on Oneida Lake, New York. Numbers of nesting pairs represent annual peak nest counts, and nests known to fledge chicks (1998-2003) are the result of nest management

Year	Nesting pairs (peak nest count)	Change from previous year (%)	Nests known to fledge chicks	No. fledged chicks	Max no. DCCO during migration
1979	0	-	-	0	27[†a]
1980	0	-	-	0	-
1981	0	-	-	0	-
1982	0	-	-	0	-
1983	0	-	-	0	-
1984	1	-	-	0	-
1985	1	0	-	1	-
1986	5	400.0	-	-	-
1987	18	260.0	-	30	1050[†b]
1988	30	66.7	-	-	-
1989	44	46.7	-	40	-
1990	62	40.9	-	80	-
1991	90	45.2	-	121	-
1992	105	16.7	-	134	-
1993	153	45.7	-	141	1600[†c]
1994	87	-43.1	-	102	-
1995	139	59.8	-	178	1615
1996	216	55.4	-	318	2498
1997	269	24.5	-	373	2697
1998	332	23.4	100	160	1881
1999	339	2.1	110	130	1964
2000	365[‡]	7.7	60	111	1395
2001	260	-28.8	162	284	1693
2002	300[‡]	15.4	66	102	1114
2003	286	-4.7	79	158	1186

† Single counts in September: a) S. R. Severinghaus, 20 Sept., CBFS unpublished; b) M. E. Richmond, 18 Sept., personal observation; c) L. G. Rudstam, CBFS, 27 Sept., personal communication

‡ High water flooded the nesting island in mid-May, reducing the annual nesting population from the initial peak nest count reported here. Post high water peak counts: 244 nests in 2000, 222 nests in 2002.

Figure 2.1. Weekly abundance of double-crested cormorants on Oneida Lake, New York, based on roost counts of adult-sized birds (breeding adults, fledged chicks, and migrants) from 1995 through 2003. The data represent actual counts conducted at dusk at the colony site (Long Island) during the active breeding period and at multiple sites around the lake during the hazing period. Roost counts consisted of three or more consecutive counts that were then averaged to derive a single value for that day/location. Multiple counts performed in the same week were averaged to derive a single weekly value for each week prior to the initiation of the hazing program, after which the highest weekly count is presented. Missing weekly values were approximated by an interpolated line connecting adjacent count data. Dashed lines represent years that preceded the hazing program. Solid lines represent years when the fall hazing program was conducted, initiated in the first week of September in all years except 2003, when hazing commenced 19 August.


Avg. no. cormorants by week
3000
2500
2000
1500
1000
500
0
1995
1996
1997
1998
1999
2000
2001
2002
2003
1-Apr
15-Apr
29-Apr
13-May
27-May
10-Jun
24-Jun
8-Jul
22-Jul
5-Aug
19-Aug
2-Sep
16-Sep
30-Sep
14-Oct
Date

In all years, the late-summer cormorant population on Oneida Lake responded rapidly to the hazing program, and numbers of cormorants dropped sharply after initiation. Not all birds left the lake, however, and weekly populations of cormorants remaining on Oneida Lake fluctuated between 20 and 400 cormorants ($\bar{x}$ = 151.7, SE = 22.9) through September in all years. Aside from occasional spikes due to the influx of new migrants, the number of cormorants remaining on Oneida Lake diminished over the 4-6 weeks of the fall hazing program, but never reached zero. Coincident with the population decline on Oneida Lake was an increase in the number of cormorants on nearby Onondaga Lake, which we observed in all years and documented in 1998-2000 (Fig. 2.2). Similar increases were not observed on the other local lakes surveyed.

Telemetry

We tracked adult cormorants tagged on Oneida Lake on 76 days in July and August of 1999 and 2000, and have compiled over 525 daytime locations, comprised of single daily locations per individual for 29 cormorants (Fig. 2.3A). These points depict both foraging and loafing/resting locations, and collectively are assumed to represent the general spatial distribution of daily cormorant activity on Oneida Lake prior to hazing. Analysis of cormorant UD during this time reveals Long Island, the nesting island and main roosting location on Oneida Lake, to be the core use area for the colony (Fig. 2.3A). Of the 30 adult cormorants we radio-tagged, 22 remained tagged and on Oneida Lake from the time of capture to the initiation of hazing in September. One cormorant left Oneida Lake shortly after capture in 1999, and was detected 80 km away in eastern Lake Ontario on 12 September. A second cormorant, trapped on the nest in June 2000, remained on Oneida Lake through 29 July and was later relocated on Cross Lake (Fig. 2.3A), where it was frequently located with a small group of cormorants throughout the remainder of the season. No additional radio-

tagged cormorants were detected on surrounding water bodies prior to the start of hazing.

Our telemetry data indicated that the onset of hazing disrupted the use of Long Island as a hub for cormorant activity on Oneida Lake. The number of radio-tagged cormorants detected by the automated receiver on Long Island in 2000 declined sharply after hazing (Fig. 2.4), analogous to the dramatic decline in the cormorant population lake-wide (Fig. 2.2). We routinely detected 14 tagged adult cormorants on and around Long Island in the month prior to the start of hazing that season. All but 3 of these left the lake by 7 September, and these 3 individuals remained on Oneida Lake through September along with the 100-200 cormorants routinely observed. These 3 cormorants were manually located and observed around the lake through the month of September, but were rarely detected by the automated receiver on Long Island after 7 September. The automated receiver did, however, detect brief visits to Oneida Lake by 3 other tagged cormorants that subsequently became residents of Onondaga Lake (see below).

Qualitative analysis of cormorant UD in the region during the hazing period reveals a strong shift to nearby Onondaga Lake. We collected 245 daytime locations over 40 days of radio tracking in September 1999 and 2000 (Fig. 2.3B), representing single daily locations per 23 individual cormorants. These locations reveal the general pattern in movement of most radio-tagged birds from Oneida Lake to Onondaga Lake, further supporting the trends evident in the count data (Fig. 2.2). Of the 9 tagged cormorants residing on Oneida Lake when hazing began on 2 September, 1999, 6 had relocated to Onondaga Lake by 12 September, 2 appeared to remain on Oneida Lake through most of the month, and 1 disappeared mid-month (Table 2.2). Cormorants left Oneida Lake much more quickly in 2000, with 10 of the 13 birds present at the

start of hazing gone from the lake within 2 days (Table 2.2). These location data corroborate the count data from both seasons (Figs. 2.1 and 2.2).

Juvenile cormorants radio-tagged in 2003 behaved similar to tagged adults during hazing and did not remain on Oneida Lake through September. Five of the 8 juvenile cormorants left Oneida Lake during the 5 days preceding the initiation of hazing on 19 August. Two of the 5 were detected on Onondaga Lake prior to the start of hazing (14 and 17 August), while the other 3 were not subsequently detected on either lake. Of the 3 birds to remain on Oneida Lake until 19 August, we located 1 on Onondaga Lake on 21 August, 1 was not located until being detected by the automated receiver on Long Island on 18 September and then was sporadically detected until 19 October, and 1 disappeared completely.

DISCUSSION

Oneida Lake is a large productive system that is intensively studied and managed for high sport fish densities. These high densities make it a popular destination for anglers throughout the northeast, and are likely the same attributes that continue to attract cormorants. The 35% annual population growth rate observed for Oneida Lake's cormorant colony from 1988 to 1998 is higher than average population growth rates reported for the Great Lakes during this same time period (1990-2000), but consistent with population growth observed in the Great Lakes during the 1980s (Weseloh et al. 2002). The initial rapid growth of the Oneida Lake colony strongly suggests the influence of immigrant adults from other sites, likely stemming from the use of Oneida Lake as a stop-over location by migrant cormorants from Great Lakes colonies in the late 1970s and early 1980s. Prior to the management program in 1998, 1994 was the only year in which negative population growth was observed for cormorants on Oneida Lake (Table 2.1). This was likely influenced by the nest

Figure 2.2. Counts of double-crested cormorants on the three lakes in central New York for 1998, 1999, and 2000. For Oneida Lake, data represent actual counts conducted at dusk at the colony site (Long Island) during the active breeding period and at all known roosting sites around the lake during the hazing period (a lakewide census). Counts at Cross Lake and Onondaga Lake were made during daylight hours as per a standard 6-lake ground survey of lakes in the region. These counts were conducted using a 3-minute time-area sampling regimen, from 4 standardized observation locations on the shoreline of each lake.

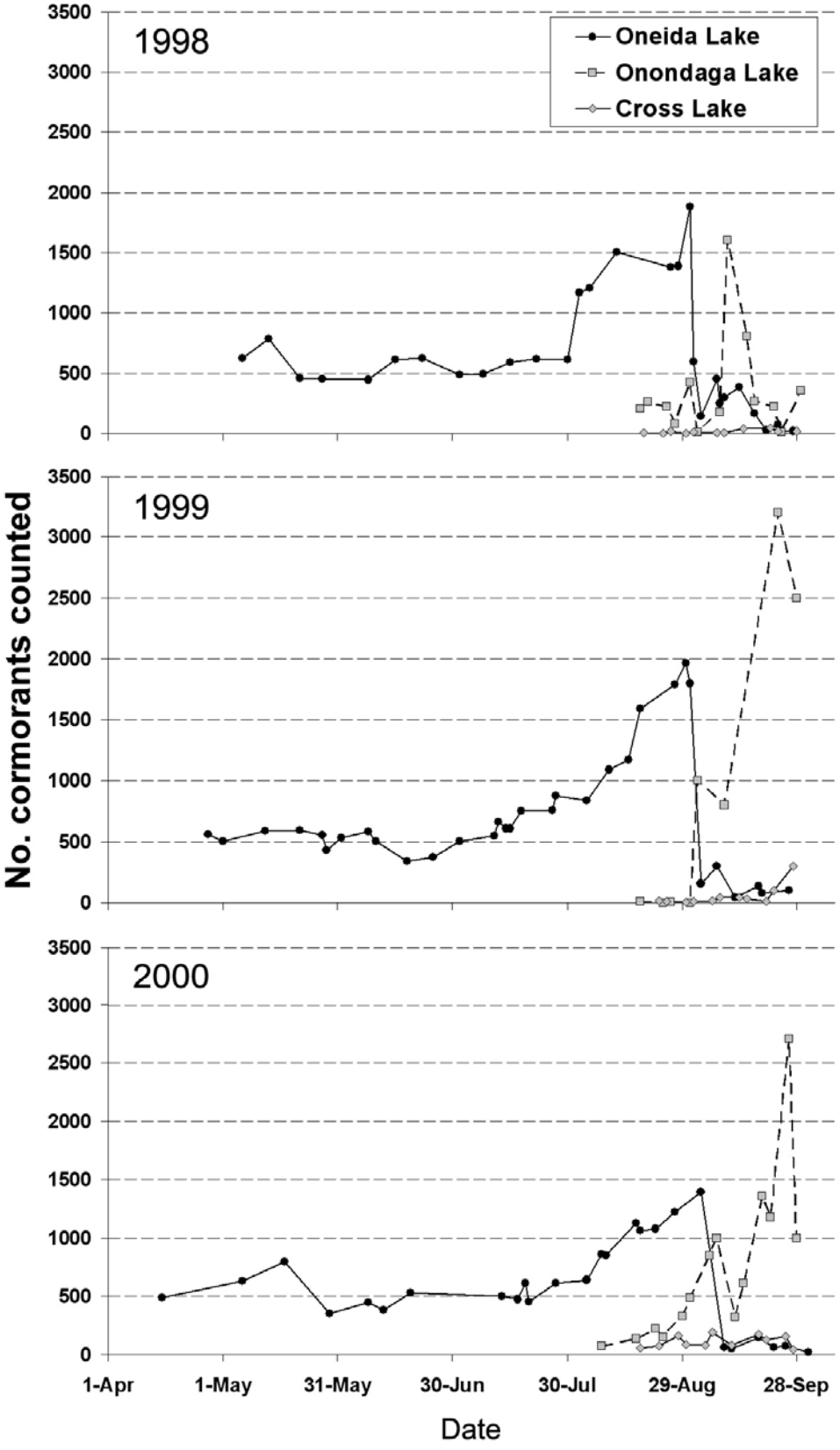
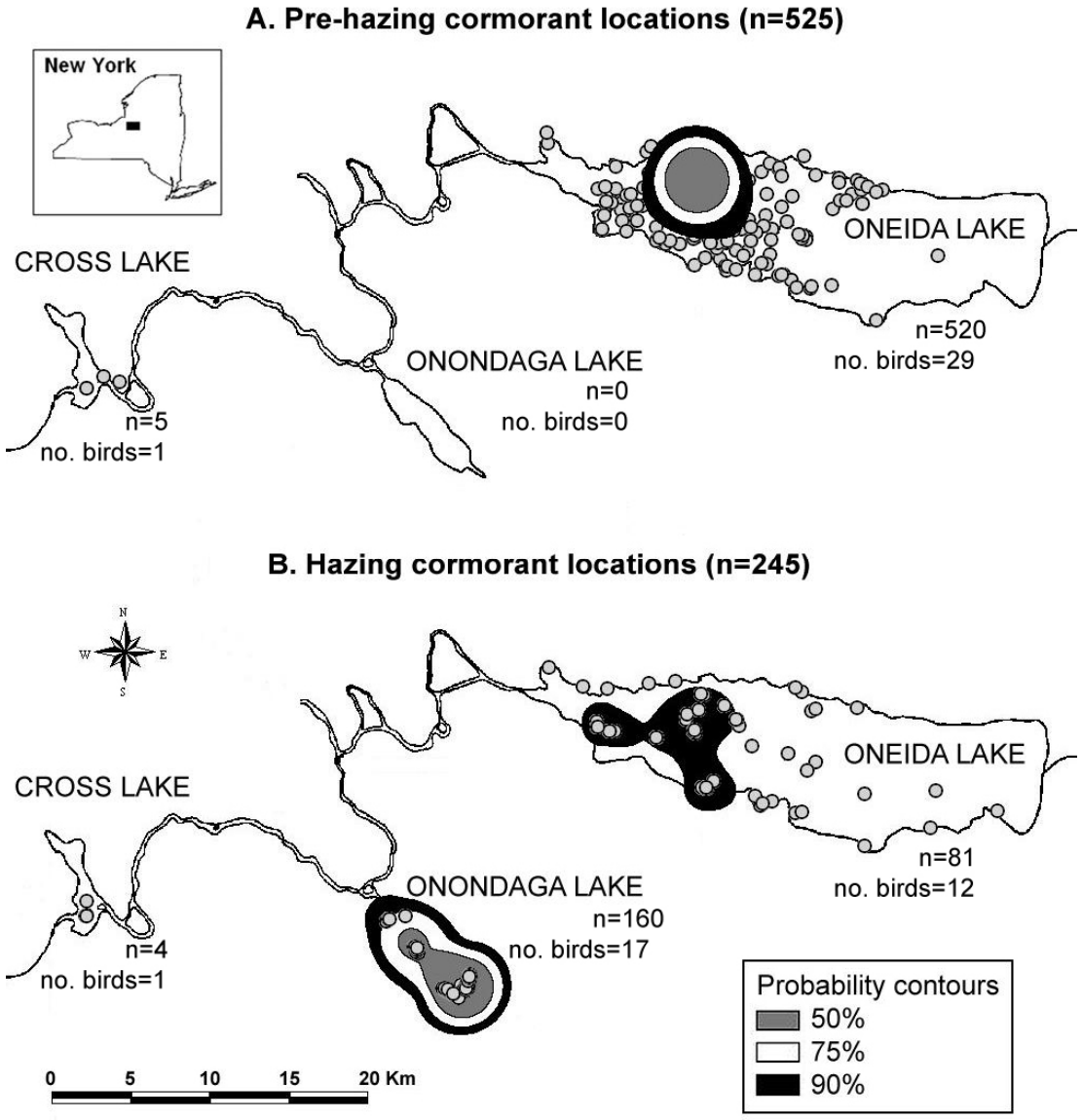

1998
1999
2000
Oneida Lake
Onondaga Lake
Cross Lake
No. cormorants counted
0
500
1000
1500
2000
2500
3000
3500
1-Apr
1-May
31-May
30-Jun
30-Jul
29-Aug
28-Sep
Date

Figure 2.3. Daily locations of radio-tagged adult double-crested cormorants in central New York (inset), depicting utilization distribution (UD) by probability contour. Data for 1999 and 2000 were pooled, and kernel methods were used to generate 50%, 75%, and 90% isopleths for all cormorants before and after initiation of the cormorant hazing program annually. A) Distribution of 29 individual cormorants in July and August, prior to hazing, indicating a UD centered around the breeding colony on Long Island in Oneida Lake. B) Distribution of 23 individual cormorants in September, after hazing was initiated, indicating a shift in the core use area representative of the relocation of most birds to Onondaga Lake.


A. Pre-hazing cormorant locations (n=525)
New York
CROSS LAKE
ONONDAGA LAKE
n=0
no. birds=0
ONEIDA LAKE
n=520
no. birds=29
n=5
no. birds=1
B. Hazing cormorant locations (n=245)
N
W
E
S
CROSS LAKE
ONONDAGA LAKE
n=160
no. birds=17
ONEIDA LAKE
n=81
no. birds=12
n=4
no. birds=1
Probability contours
50%
75%
90%
0 5 10 15 20 Km

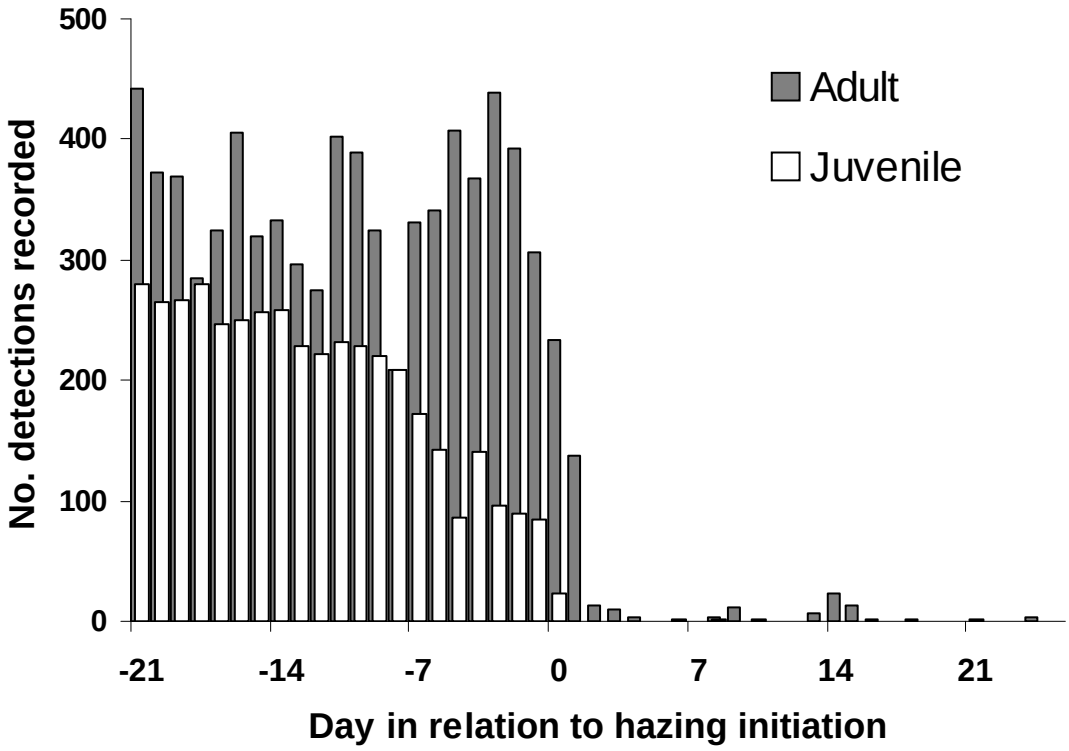


Figure 2.4. Cumulative number of detections by day for 14 radio-tagged adult cormorants in 2000 and 8 radio-tagged juvenile cormorants in 2003 on Oneida Lake, New York. The time-span on the X-axis represents approximately the 3 weeks before and after the initiation of hazing each year, represented as day zero (5 September in 2000, 19 August in 2003). Thus, dates depicted are 15 August-30 September 2000, and 29 July-13 September 2003.

Table 2.2. Location of individual adult cormorants from radio tracking by date. The heavy line represents the start of hazing. Lake names are coded:
E = Oneida Lake, G = Onondaga Lake, and X = Cross Lake. Detection data from the automated receiver are included to augment Oneida Lake locations in 2000.

	Cormorant																							
	1999									2000														
Date	A	B	C	D	E	I	K	L	O	P	Q	R	S	T	U	V	W	X	Y	Z	AA	BB	DD
27-Aug										E	E	E	E	E	E		E	E	E	E	E		E
28-Aug	E	E	E	E	E	E	E	E	E	E	E	E	E	E	E		E	E	E	E	E		E
29-Aug	E		E	E	E	E	E	E	E	E	E	E	E	E	E		E	E	E	E	E		E
31-Aug	E	E	E	E	E	E	E	E	E	E	E	E	E	E	E	E	E	E	E	E	E	X	E
1-Sep				E	E	E	E	E	E	E	E	E	E	E	E	E	E	E	E	E	E		E
2-Sep	E		E	E	E	E	E	E	G	E	E	E	E	E	E	E	E	E	E	E	E		E
3-Sep	E		E	E	E	E	E	E		E	E	E	E	E	E	E	E	E	E	E	E	X	E
4-Sep	E			E		E				E	E	E	E	E	E	E	E	E	E	E	E		E
5-Sep	E		E		E	E	E	E		E	E	E	E	E	E	E	E	E	E	E	E		E
6-Sep										E	E/G	E/G		E/G	E		E	E	E	E	E/G		G
7-Sep	E		E		E	E				E					E								
8-Sep		G		G	E	E	E		E		G	G	G	G	G			G	G	G	G		G
9-Sep					E	E				E						E	E		E				
10-Sep		G		G			E	E		E	G	G	G	G	G	E	E	G	G	G			G
11-Sep	E				E	E	E		E														
12-Sep	E	G	G	E/G	E	E	G	G	E/G													X	
13-Sep										E	G	G	G	G	G	E		G	G	G	G		G
14-Sep	E				E					E	G	G	G	G	G	E	E	G	G	E	G	X	G
15-Sep		G	G	G			G	G	G		G	G	G	G	G	E		G	G	G	G		G
17-Sep		G	G	G			G	G	G	E						E	E	E					
19-Sep										E						E	E	E				X	
20-Sep										E	G	G	G	G	G	E	E	E/G	G	G	G	X	G
21-Sep																						X	
22-Sep		G	G	G			G	G	G	E	G	G	G		G	E	E*	G	G	G	G		G
24-Sep		G	G	G	E		G	G	G	E	G	G	G		G	E		G	G	G	G		G
25-Sep		G	G	G	G	E	G	G	G	E						E							
26-Sep																						X	
27-Sep											G		G		G			G		G	G		G
28-Sep										E	G		G		G	E		G	G	G	G	X	G
29-Sep		G	G	G			G		G				G		G	E		G		G	G		G
1-Oct																E							
2-Oct											G		G		G	E		G	G	G	G		G
19-Oct																E							
20-Oct											G	G							G				

"E/G" represents cormorants detected on Oneida Lake in the morning (0630-0900 hrs) and on Onondaga Lake that afternoon (1400-1830 hrs
* 22 September 2000: bird W found dead of gunshot on north shore of Oneida Lake

management experiments conducted for 3 years prior. However, numbers of cormorant nests at sites across Lake Ontario and Lake Huron also fell that same season (Blackwell et al. 2002; Ridgway et al. 2006), perhaps suggestive of a more large-scale perturbation.

While the Oneida Lake breeding population continued to increase in 1999 and 2000, the annual rate of growth declined sharply in those first two years following the inception of the management program. Given the relatively small size of this colony and the ample forage base and nesting space available, density-dependent effects observed elsewhere (Ridgway et al. 2006) are not likely to have impacted the Oneida Lake colony by 1999, leaving the management program as the most plausible cause for declining growth rate. Because nest control and fall hazing were instituted simultaneously, it is not possible to conclusively parse the effects of these two programs on breeding effort in subsequent years. Due to the late timing of hazing in relation to the nesting period, however, we speculate that the reduced reproductive success from the nest control effort likely had a greater impact on the number of cormorants returning to Oneida Lake than the fall hazing effort. High water events of 2000 and 2002, which flooded the colony, resulted in more drastic declines in following years and confounded our ability to quantify and interpret the behavioral response of breeding cormorants to the management actions. In general, however, the 14 and 22% reduction in annual breeding population size observed on Oneida Lake between 1998 and 2003 (based on peak nest counts from 1998 and 2000, respectively) are comparable to the 25% decline resulting from egg oiling observed at the much larger colony on Little Galloo Island in Lake Ontario during the same time period (Farquhar et al. 2004). The goals of nest management on Oneida Lake and Little Galloo Island differed in scope in that 100 nests, approximately 1/3 of the colony, were left undisturbed on Oneida Lake, while all accessible nests on Little Galloo

Island were treated to prevent hatching (Farquhar et al. 2000, 2003). Allowing a large portion of the colony to successfully reproduce is likely to favorably impact perception of site quality by breeding cormorants, especially when success rates are considerably lower at neighboring sites, such as Little Galloo Island.

The immediate response of cormorants to fall hazing on Oneida Lake was readily apparent, and consistent with results of similar harassment programs at winter roost sites in Mississippi (Mott et al. 1998; Tobin et al. 2002). Cormorants subjected to static deterrents, bombardment by pyrotechnics at roost sites, and daytime hazing at all locations around the lake, generally left the lake altogether in preference for a different lake where they were not exposed to hazing. Counts of cormorants through late summer and fall indicated that the majority of birds that normally resided on Oneida Lake relocated to Onondaga Lake, a smaller lake (11.9 km^2) situated approximately 20 km to the southwest of Oneida Lake (Fig. 2.3). While Onondaga Lake is situated in an urban environment and lacks islands suitable for nesting, we commonly observed cormorants loafing and roosting in wooded shoreline areas that are generally inaccessible to the public. Despite the proximity of the two lakes, the telemetry data suggest that once on Onondaga Lake, cormorants tended to remain there rather than returning to Oneida Lake to forage (Table 2.2). Furthermore, the telemetry and count data indicate that the hazing program served to shift the core use area for the population to Onondaga Lake rather than prompting cormorants to continue, or initiate, their southward migration. This observation is similar to scenarios described for non-lethal management at southern aquaculture facilities, where use of an alternate foraging location by displaced birds, albeit one that is usually intentionally stocked with alternate prey, has been described as a means to facilitate harassment efforts on target ponds (Erwin 1995; Mott and Boyd 1995).

Whereas fall hazing was successful in removing the majority of cormorants from Oneida Lake through the month of September, an average of 150 birds remained and utilized various night roosts around the lake. Given the non-lethal nature of the program through 2003, the large size of Oneida Lake, and the fact that there were a limited number of boats on the lake simultaneously hazing birds, persistent cormorants apparently evaded the hazing crews by continually moving from roost to roost. Telemetry results from 1999 and 2000 revealed that some portion of this September population consisted of adult birds that had bred on the lake in that season. At the time we hypothesized that the majority of the remaining cormorants were fledged chicks from the current season that were reluctant to leave their natal system. The radio-tagging of 8 juveniles in 2003 was designed to test this hypothesis, and ultimately disproved it. The majority of juveniles left Oneida Lake as the adults did, and presumably integrated with the adult population through fall migration. Notably, 2 of the 5 telemetered adult cormorants that remained on the lake in 1999 and 2000 were those that, prior to the initiation of hazing, displayed fidelity to relatively unique foraging territories that were farther from Long Island than those of their conspecifics (Coleman et al. 2005). These two individuals were commonly in the presence of many other cormorants at these alternate loafing and foraging sites, but because the others were not marked, we do not know the degree to which these birds contributed to the persistent September population on the lake. It may be that these individuals were less disturbed by the hazing practices on and around Long Island because they were less reliant on the island, and that region of the lake, in their daily movements. In terms of spatial utilization of the lake, we found that the same general areas of Oneida Lake were used by tagged cormorants prior to and during the hazing period (Fig. 2.3), reinforcing the selection of those sites for their habitat qualities, regardless of the distance from Long Island (see Coleman et al. 2005).

To our knowledge, the management actions we describe are the first such efforts to incorporate nest control and an intensive, non-lethal hazing program to address a rapidly expanding population of double-crested cormorants on a lake in northern breeding grounds. Despite the differences in the scope and scale of this project compared to previous accounts from the southeastern U.S., our conclusions from the hazing component of this effort are consistent with those gleaned from similar exercises on commercial aquaculture ponds: successful daily harassment and roost disruption requires a considerable commitment of time, effort, and resources. However, as large-scale cormorant management programs have spread through the Great Lakes states and provinces (NYSDEC 2004; MDNR 2005; USDA/APHIS 2004, 2005; OMNR 2006), popular support and funding for these types of projects have likewise increased. The nest control and non-lethal hazing techniques we present here succeeded in achieving immediate prescribed goals on Oneida Lake and reduced the predation pressure on fish stocks by an estimated 40% compared to that experienced at the 1997 cormorant population level (VanDeValk et al. 1999; Coleman 2009, Chapt. 2). Analysis of the response of sport fish populations to the reduced consumption pressures resulting from this management program is currently in preparation (see Coleman et al. 2008). For the first time since 1995, common terns also began to nest on Long Island in 2003, and have capitalized on the nesting space available to them on that island each year since (Coleman and Richmond, unpublished data).

Public perception of cormorant management on Oneida Lake was favorable. When asked if cormorants were affecting fish populations in the lake, Oneida Lake angler responses to a standard creel survey indicated that the perception of a significant impact of cormorants on the fishery increased from 23% of respondents in 1995 to 37% and 38% in 1997 and 1998, respectively (CBFS, unpublished reports). By 2003, perception of cormorants by the local angling community had changed

dramatically following a season with unprecedented high targeted-catch rates of 0.58 walleye/angler hour (VanDeValk et al. 2004), and perception of negative cormorant impacts declined to the extent that the birds were rarely incriminated by anglers, regardless of the anglers' daily success (S. D. Krueger, CBFS, personal communication). Concomitantly, public acceptance of cormorant hazing activities may also have engendered an endorsement of similar such activities by "well intentioned" individuals of the general public. Observations of boaters driving at cormorant flocks on the water and venturing close enough to day and night roosts to flush birds increased in frequency over the years of this study (J. Coleman, personal observation). Such unauthorized hazing was common in August of 2003, and potentially contributed to the premature egression of adult and juvenile cormorants observed that year.

MANAGEMENT IMPLICATIONS

The methods we describe here represent a soft approach to cormorant management that resulted, in part, from the protected status of the double-crested cormorant in 1998 prior to the finalization of a public resource depredation order (USDI/FWS 2003). Other concerns that shaped the implementation of this approach to managing cormorants were the proximity of these birds to a large common tern colony, and the socio-economic value of Oneida Lake as an important recreational resource. Whereas the use of lethal control to most effectively reduce adult cormorant populations, and their potentially negative impacts, has previously been discussed (Bédard et al. 1995, Blackwell et al. 2000), culling was not considered to be appropriate for the initial phase of the Oneida Lake management project. While it might have been possible to eventually reduce the resident population to 100 pairs using the non-lethal techniques we describe, the time commitment would likely have

been considerable. The pressures asserted by local stakeholder groups demanding further action, corroborated by a second citizen cormorant task group convened in 2003, necessitated the development of a more aggressive policy for 2004 (NYSDEC 2004).

The apparent similarity between the ultimate response of breeding and migrating cormorants to the two constituent elements of this program is noteworthy. Nest control and fall hazing both appeared to negatively impact the number of cormorants that returned to Oneida Lake to breed and stop-over in subsequent seasons. Severe storm events and subsequent high lake levels, however, made it difficult to definitively conclude the extent to which management affected cormorant numbers over the 6-year period of this study. While high water in 2000 and 2002 likely affected return rates for breeding adults in subsequent seasons, the effect of annual nest control on breeding effort was readily apparent in the reduced rate of colony growth in 1999 and early 2000, prior to the flooding. These same high water events also confounded our ability to assess the sustained effects of fall hazing in subsequent years, as the reduced number of cormorants breeding at the Oneida Lake colony likely affected population levels through to the initiation of hazing. The hazing program did not appear to deter use of Oneida Lake as a destination for non-resident cormorants during their initial migratory movements in the region. The aggregation of cormorants on Oneida Lake starting in mid-July followed the same general pattern each season, affected only by the weather conditions that naturally cue southward movements in birds. Thus, non-lethal harassment alone, targeting non-resident cormorants in late summer, may not be the most effective long-term strategy to address predation impacts on a sport fishery, at least not on a lake the size of Oneida Lake. It is increasingly apparent that concerns over cormorant impacts must address regional population goals to be most effective. The results from this study, and those

incorporating satellite telemetry in central New York (Werner et al. 2001; Dorr et al. 2002, 2003), indicate the high degree to which cormorants rapidly move between breeding colonies and day roosts throughout the region, especially in the pre-migratory period of late summer. Actions that moved birds off of specific sites redistributed them to other locations in the region. Resource managers and users have become increasingly intolerant of conspicuous cormorant populations, even on seemingly favorable systems like Onondaga Lake, where human-cormorant interactions are minimal. Therefore, unless they relocate to coastal waters, where large populations of cormorants are more commonplace, displaced cormorants are just as likely to be unwelcome at new destinations as they were at the original site. While an economic evaluation of the management program described here is beyond the scope of this paper, the expansion of hazing operations to cover multiple waterbodies in a region may become physically and financially impractical to undertake on a long-term basis. Unlike private aquaculture facilities, large lakes are usually public resources, managed by state or regional agencies. Thus, given the potentially substantial staffing and fiscal investment necessary to conduct cormorant management efforts, the decision to pursue non-lethal cormorant management to reduce predation pressures on aquatic resources is a decision that requires strong public support.

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CHAPTER 3:

AN ASSESSMENT OF THE PREDATOR-PREY DYNAMICS OF CORMORANTS, WALLEYE, AND YELLOW PERCH IN ONEIDA LAKE, NEW YORK: SIZE SELECTIVITY, TROPHIC INTERACTIONS, AND THE IMPACT OF MANAGEMENT FROM 1998-2005[1]

Abstract: Coincident with an increasing double-crested cormorant population on Oneida Lake, New York, were declines in numbers of sport fish in the 1990s, most notable in walleye and yellow perch. A cormorant control program was initiated in 1998, partly intended to mitigate the impact of cormorant predation on the fishery by reducing the reproductive success of residents and preventing the accumulation of migrant populations on the lake in late summer and fall. Cormorant diet sampled in 1994-2003 (n = 2375 regurgitated boluses, n = 137 stomach samples) included 27 different species, but consisted of 58-72% walleye and yellow perch by weight annually, and 64% of the total prey biomass across the 9 years of the study. The availability of abundance estimates of all age classes of these two species allows for calculations of selectivity of cormorants to different age classes using the relativized electivity index (E^*). Cormorants generally selected age 1-3 walleye, and age 2-4 yellow perch, with peak selectivity for age-2 walleye and age-3 yellow perch. The peaks of the electivity curves align when plotted against fish girth (max. circumference), but not when plotted against fish total length, which suggests that fish girth is the main determinant of maximum size of fish that cormorants will consume. White perch and ictalurids were less prevalent in the samples than expected based on

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estimated availability (relative abundance in standardized gillnets), possibly due also to limitations of gape and the morphological characteristics of the different species. The cormorant control program resulted in a mean reduction in predation pressure on fish populations of approximately 47% from the 1997 level (range: 30-83%) in 1998-2005. The reduction in cormorant feeding days coincided with an increase in abundance of the adult populations of both the walleye and yellow perch. For walleye, this also coincided with an increase in survival from age 1 to age 4, although this increase is larger than expected from the level of cormorant reduction alone. Other factors, such as an increase in gizzard shad and white perch since 1997, which provide an alternate prey for cormorants, may have contributed to lower cormorant predation on walleye. Alternatively, recruitment of walleye to age 1 could have been larger than was revealed in our trawl samples, possibly also a response to increases in gizzard shad. The increase of yellow perch survival from age 1 to age 3 was not as large, but was more consistent with our expectations. Although the observed increase in adult populations of both percid species is consistent with expectations following cormorant control, the magnitude of the increase in walleye was larger than expected based on the degree of decline in cormorant feeding days.

Key words.- cormorant, diet, food-web, harassment, hazing, impact, interaction, management, nest control, Oneida Lake, *Phalacrocorax auritus*, predator-prey, recruitment, regurgitant, relativized electivity, selectivity, walleye, yellow perch

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Trophic interactions result in direct and indirect impacts to populations and are fundamental to inter- and intraspecific community dynamics (Lindeman 1942, Berryman 1992, Polis and Strong 1996). Top predators can impact community

structure in aquatic systems (Carpenter et al. 1984, McQueen et al. 1989), but determining causality behind observed population-level changes can be very difficult, especially in large, complex systems. Even in instances where species are newly introduced to an existing system/food-web, compensatory mechanisms, indirect pathways, and data quality issues can confound the ability to elucidate the mechanisms affecting population dynamics. The effect of cormorant predation on populations of economically important wild fish species, for example, is of great interest in both North America and Europe, where cormorant populations have grown rapidly in the 1980s and '90s. However, a definitive understanding of the nature of cormorant impacts on fish populations, that can hold up to rigorous critique by various stakeholders, has been elusive due to the complexity of aquatic food-webs, the diversity of species assemblages and in the lakes in question, the flexibility in cormorant prey choice, and the lack of suitable background data (Suter 2000, Wires et al. 2001, 2003; Reed et al. 2004; Diana et al. 2006). While some studies have suggested that cormorants may negatively impact fish populations (Birt et al. 1987, Burnett et al. 2002, Lantry et al. 2002, Rudstam et al. 2004, Winfield et al. 2005), the majority of studies indicate that cormorants do not impact species with any sport or commercial value (see review by Trapp et al. 1999, Belyea 1999, Suter 2000, Wires et al. 2001, Reed et al. 2004, Diana et al. 2006). The main criticism of the research supporting negative impacts is that the authors fail to adequately relate cormorant prey consumption to population–level impacts to fish, mostly due to a lack of comprehensive fish data (Wires et al. 2001, Diana et al. 2006). Comprehensive knowledge of prey populations are a critical element to the study of the predator impacts, and attempts to understand complex species interactions are greatly facilitated by long-term trends that integrate short term fluctuations associated with population stochasticity (Mills and Forney 1988, Brown et al. 2001). Therefore, a

study of cormorant impacts on fish populations necessitates a study location with long-term population data, which includes a comprehensive record of the biotic and abiotic factors that also affect fish population dynamics. One such location is Oneida Lake, New York.

Oneida Lake, in central New York, has been actively managed for decades, and is considerably different than it was at the time of European contact and early American settlement in the region. Once renowned for American eel (*Anguilla rostrata*), Atlantic salmon (*Salmo salar*), whitefish (*Coregonus* spp.), black bass (*Micropterus* spp.), northern pike (*Esox lucius*), and chain pickerel (*Esox niger*), Oneida Lake has been a premier walleye (*Sander vitreus*) fishery since the mid 20th Century, when water level regulation and wetland destruction resulted in the near extirpation of other top predators in the system, namely eel, northern pike, and pickerel (Adams and Hankinson 1928, Forney 1977). Throughout the many transitions in piscivore assemblages, the yellow perch (*Perca flavescens*), a keystone species in Oneida Lake (Mills and Forney 1988), has remained prevalent and comprises the foundation of the forage base (Forney 1974, 1977, 1980). Over time other "forage" species entered the lake, including the white perch (*Morone americana*) in the late 1940s and gizzard shad (*Dorosoma cepedianum*) in the early 1950s (reviewed by Forney 1977), adding to the diversity of the prey base. In the recent past, management of the walleye population has focused on maintaining a balance with populations of its main prey, the yellow perch (perch) (Forney 1980), and the trophic links and interaction dynamics between the two species are well documented for Oneida Lake (Forney 1974, 1977; Nielsen 1980; Mills et al. 1987; Mills and Forney 1988; Rudstam et al. 1996; Hall and Rudstam 1999). Annual walleye production matched that of perch through the 1960s and 1970s (Mills et al. 1987), and the stability of the adult walleye stock through the '60s and '70s indicated a

sustainable relationship between walleye and prey stocks (Forney 1977). After two decades studying walleye-perch interactions, Forney (1980) developed walleye harvest guidelines intended to maximize yield of adult fish for recreational angling while maintaining the balance with prey populations by reducing the destabilizing effects of stochastic perch abundance. The long-term average biomass for adult walleye (age-4+ yr) in Oneida Lake is approximately 18 kg ha^{-1}, and walleye rely heavily on the production of YOY forage fish to the extent that the impact of predation can affect young fish recruitment (Hall and Rudstam 1999).

Coincident with the publication of management guidelines for walleye, a new top predator, the double-crested cormorant (*Phalacrocorax auritus*), was increasing in abundance on Oneida Lake, first as a non-resident migrant, then as a resident breeder starting in 1984 (Claypoole 1988). Unlike predatory fish, which are vulnerable to larger fish at early life stages, piscivorous birds are exempt from the depredation feedback processes that regulate typical predator-prey interactions within an aquatic system. Once the breeding population was established, the double-crested cormorant (cormorant) colony grew geometrically, by rates similar to or exceeding those reported for other colonies throughout the Great Lakes region (Fowle et al. 1999; Weseloh et al. 2002; Coleman 2009, Chapt. 2). The number of migrants visiting the lake in late summer and fall likewise increased, adding to the predation pressure exerted on fish stocks by breeding adults and chicks. Cormorants are generally considered to be opportunistic feeders, and exhibit variation in diet and foraging range depending on colony location and seasonal prey availability (Craven and Lev 1987; Ludwig et al. 1989; Campo et al. 1993; Blackwell et al. 1995, 1997; Ross and Johnson 1995; Neuman et al. 1997; Coleman et al. in review). As annual cormorant abundance increased on Oneida Lake, adult stocks of walleye and perch both declined, such that by the mid 1990s both species were approximately one third as abundant as their

average population level over the previous 35 years (VanDeValk et al. 2001). The most likely explanation for declining abundance of percids (hereafter referring to walleye and yellow perch) was the impact of cormorant predation.

Rudstam et al. (2004) detailed the evidence supporting the link between cormorant predation and percid population declines in Oneida Lake, the main points being: 1) the coincidental timing of the growth of the cormorant population and declining percid abundance, 2) the observed increase in mortality of subadult walleye and subadult yellow perch, the age classes often consumed by cormorants, 3) the amount of fish calculated to have been consumed by cormorants was approximately the same as the number of missing fish in each age class based on projected recruitment from age-1 abundance to adult stock, and 4) a population model revealed that the increased subadult mortality observed in both species was capable of impacting adult population on the order of what was observed. The long-term population data available for Oneida Lake percids reveals a correlation between summer trawl catches of age-1 yellow perch and walleye, and future recruitment to age-3 (yellow perch) and age-4 (walleye) (Forney 1980, Rudstam et al. 2004). This relationship remained moderately consistent for almost 30 years, before deviating in the early 1990s. The 1989-1997 year classes recruited fewer adult fish than expected from this relationship indicating increased mortality of subadults, attributed to cormorant predation as per point 3 above (Rudstam et al. 2004, Irwin et al. 2008).

As the double-crested cormorant population on Oneida Lake became increasingly conspicuous, strong public concern also began to grow regarding the potential for detrimental impacts to sport fishing and island habitats. By the mid-1990s it became evident that cormorants had begun to exceed public wildlife acceptance capacity (Decker and Purdy 1988) in the region, and the New York State Department of Environmental Conservation (NYSDEC) developed management

objectives for the control of both resident and migrant cormorant populations on Oneida Lake. To further protect the adult walleye population, harvest restrictions were also implemented from 2001-2005, in accordance with the recommendations established by Forney (1980) (see Methods).

In this paper we revisit the status of walleye and yellow perch populations in Oneida Lake following the first 8 years of an ongoing cormorant management program. Rudstam et al. (2004) described the growing cormorant population as a natural perturbation, and thus as an opportunity for gaining insight into predator-prey interactions and food web dynamics (Carpenter 1990). Here, we approach the subsequent reduction of the cormorant population that resulted from a collaborative management program in that same light; in effect, treating the addition and gradual removal of cormorants to an aquatic system as a type of "press" perturbation experiment (Bender et al. 1984). Based on the 4 lines of evidence presented by Rudstam et al. (2004), we hypothesized that the reduced cormorant impact resulting from the management program would produce some measurable results, namely: 1) an increase in survival from age-1 to adult stage (age-3 for perch, age-4 for walleye), and 2) an increase in adult percid populations in the lake. To assess the changing consumptive pressures resulting from the management program, the behavioral response of cormorants was closely monitored (Coleman 2009, Chapt. 2), and concurrent detailed population and dietary studies of the fish species in the lake were conducted. We demonstrate the progression of cormorant predation pressure exerted on the Oneida Lake fish community, and we present the results of 9 years of cormorant diet study, including an analysis of age selectivity in percids. Our results elucidate the age-specific impact of cormorants on percids, and reveal the morphological characteristics that determine cormorant prey selection, and thus the size refuge parameters, in fusiform species. Given our understanding of age-specific

impact, and the influence of the cormorant management program, we re-analyze the historic recruitment dynamics for walleye and yellow perch to see how the recent reduction of cormorant predation has affected recruitment and the standing stock of adult percids. Because harvest regulations for adult walleye were also changed during the study period, we use a simple population model to illustrate the added effect of harvest management on the adult population, and predict the long-term results of different management scenarios. Lastly, we incorporate results from these analyses of community dynamics to speculate on additional factors that may have contributed to the rapid declines observed in walleye and yellow perch in Oneida Lake in the early 1990s.

METHODS

Study area

This study incorporates approximately 50 years of fish population data and over 20 years of cormorant count data collected at Oneida Lake, New York. Oneida is a large shallow lake, with a surface area of 207 km^2, a maximum depth of 16.8 m, and an average depth of 6.8 m. Walleye have been stocked in Oneida Lake since 1893 (Forney 1975), and the lake supports one of the most valuable sport fisheries in New York (Connelly and Brown 1991). The comprehensive long-term data available for the fish of Oneida Lake, particularly for walleye and yellow perch, make these fish populations two of the most well-studied in North America, providing an excellent foundation for the study of cormorant-fish interactions in a lake system. Walleye and yellow perch are two of the most numerous fish species in the lake, and generally account for ½ to ¾ of all fish caught in annual, standard assessment gill net surveys since 1958 (VanDeValk et al. 2006).

Cormorant diet and selectivity

Cormorant diet has been studied since 1988 at Oneida Lake (CBFS, unpublished data), but for this study we focus on diet monitored from 1994–2003 through examination of chick regurgitant (1994-1996, and 1998-2003) and stomach contents (1995-1996, 2001-2003). Regurgitant was collected on the nesting islands at approximately weekly intervals when chicks were present, (late May to mid-August), and stomach samples were used to supplement diet data in spring and fall when regurgitant was not available. Prey items were identified to species and total lengths measured when possible. Fish too digested to measure were assigned average lengths for the same age cohort from diet samples or from fish collected concurrently in sampling gear. Age of prey was determined from scales for partially digested specimens, or assigned by comparison to known lengths of fish collected and aged for standard assessment sampling in the same season. Selectivity for different age classes of walleye and yellow perch was calculated from proportions in diets and proportions in the lake from sampling gear. We used the relativized electivity (E^*) index of Vanderploeg and Scavia (1979), as further recommended by Lechowicz (1982) and Confer and Moore (1987). We considered only summer diet samples (May-July) to quantify selectivity since these data were available for most years of the study (see below for details of fish data). The electivity coefficient E^* is defined between -1 and +1, with neutral electivity indicated by a zero value. We plotted mean electivities for each age class by both length and girth of walleye and yellow perch to explore selectivity based on prey size and morphology. Girth values represent the maximum circumference of a fish, and were determined using a length-girth relationships derived from walleye (n = 48) and yellow perch (n = 160) caught in standard gillnet sampling at Oneida Lake in 1994 (walleye: girth [mm] = 0.479(length [mm]) - 0.516,

$R^2 = 0.97$; yellow perch: girth [mm] = 0.665(length [mm]) - 4.056, $R^2 = 0.91$; L. G. Rudstam, unpublished data).

Management actions

Between 1998 and 2005 there were two management programs enacted by NYSDEC that were designed to positively impact sport fish populations in Oneida Lake: 1. cormorant control, and 2. regulations on walleye harvest. The main objective of cormorant management during this time period was the reduction in the number of both resident and migrant double-crested cormorants on the lake through summer and fall months. From 1998 to 2003 this program had two goals: 1. to limit annual reproductive success to 100 nests, and 2. to move cormorants off of the lake in late summer, after the breeding season, using various harassment/hazing techniques. This adaptive management plan was a coordinated effort between the New York Cooperative Fish and Wildlife Research Unit (NYCFWRU) at Cornell University, and the United States Department of Agriculture-Animal and Plant Health Inspection Service - Wildlife Services (APHIS-WS). The target population size for cormorants on Oneida Lake was based on the recommendations of a citizen's task group convened in 1994, and on the goals established by NYSDEC for maintaining the diversity of colonial waterbirds breeding on Oneida Lake (Chipman et al. 1998; Miller 1998; Coleman 2009, Chapt. 2). The nest control program initially consisted of weekly egg and nest removal (1998-1999), then of weekly egg oiling, where food-grade corn oil was applied to eggs in all but 100 nests, effectively addling them (2000-2003) (Gross 1951, Bédard et al. 1995). Hazing techniques used to frighten cormorants in late summer and fall were similar to those used successfully in the southeastern United States to disperse wintering cormorants from aquaculture facilities (Mott et al. 1998, Tobin et al. 2002, Barras and Godwin 2005), and included pursuit of birds by boat, the use of pyrotechnic noise-makers to disrupt flocks of birds, and the installation of static

scaring devices, such as propane exploders, inflatable human effigies, and silver Mylar® tape, on roosting or loafing areas (Chipman et al. 1998, 2000; Coleman 2009, Chapt. 2). Starting in 2004 the program was expanded to further reduce cormorant presence and impact on Oneida Lake by allowing only target number of 100 cormorants to remain on the lake through the entire season and preventing all reproduction through egg oiling and nest removal (NYSDEC 2004).

Through the 1980s and 1990s, the size limit for legal harvest of walleye in Oneida Lake was 380 mm (15 in.), with a 5 fish creel limit. Concern over declining adult populations prompted a change to harvest regulations from October 2001 to October 2005, increasing the minimum size to 457 mm (18 in.), and a 3 fish daily limit, which decreased harvest of adult walleye (VanDeValk et al. submitted). With 100-165 million fry stocked annually, changes to adult survival resulting from the angling regulations are unlikely to have impacted annual abundance of walleye fry in the lake (VanDeValk et al. 2007). Yellow perch are not stocked, and harvest regulations allow for a maximum of 50 fish per day with no minimum size requirement.

Cormorant abundance and consumption model

To better assess cormorant consumptive pressures on Oneida Lake, we used a simple bioenergetic approach to model total annual consumption based on daily food requirements from published literature and annual count data collected from 1979 to 2005 (Coleman 2009, Chapt. 2). Three groups comprise the annual cormorant population on Oneida Lake: 1) breeding adults that arrive in early spring, 2) juveniles reared on the lake, and 3) non-resident migrants that inhabit the lake beginning in late July. Biologists with the Cornell Biological Field Station (CBFS) and the NYCFWRU have counted cormorant nests and chicks annually on Oneida Lake, starting with the first nest in 1984. From 1995-2005 adult and juvenile cormorants

were counted weekly, often multiple times per week, to assess breeding success and monitor the influx of migrants to Oneida Lake. We conducted counts by boat using binoculars, generally at a distance of 75-150 m from the roost, and counted birds at least 3 full times to derive an average for each location. Counts were made at dusk, when cormorants were roosting, and locations were either low islands with minimal vegetation or tall lakeside trees, both of which provided unobstructed access to resting and perching birds. Counts were conducted at all known historic loafing and roosting sites around the lake, and are believed to represent a lake-wide census of the population.

The presence of migrating cormorants in central New York has been documented as far back as 1865 (Stoner 1932), and occasional sightings of small numbers of migrants on Oneida Lake were reported through the mid-20th Century (e.g., M. Zardus 1955, CBFS, unpublished data). Cormorant abundance on Oneida Lake remained very low through the 1960s and 1970s, and only 4 reports of between 1 and 12 individuals exist for this period prior to 1978 (C. M. Adams 2001, CBFS, unpublished data). Between 1979 and 1995, cormorants were counted 3 times on Oneida Lake, corresponding with a period of dramatic population growth throughout Great Lakes colonies (Weseloh et al. 1995). Cormorants were counted in late September 1979, 1987, and 1993, resulting in data gaps for the 1980's and early 1990's. Mid to late September is when the peak counts of cormorants were obtained in 1995-1997 (Coleman 2009, Chapt. 2), so we assume that the single counts in '79, '87, and '93 approximate peak cormorant numbers in those seasons. Assuming further that the number of migrants stopping at Oneida Lake was correlated with the number of cormorants breeding on Lake Ontario, a proxy for the regional population, we estimated annual migrant populations for the 1980s and early 1990s by regressing the number of breeding adults for Lake Ontario colonies from 1975-1997 (Weseloh et al.

1995, 2002) on the September counts for 1979, 1987, and 1993, and the peak fall counts on Oneida Lake prior to the initiation of the migrant hazing program (1995-1997). A population of 0 birds was imposed for Oneida Lake for 1975-1978. A simple linear regression revealed the formula: $y = 0.05x + 71.70$ ($R^2 = 0.92$), where x is the number of breeding adults on Lake Ontario (twice the number of nests) and y is the peak fall population predicted for Oneida Lake. While this model fit the observed data well for 1979 and the mid 1990s, it estimated approximately half the number of birds counted in 1987, suggesting that the use of Oneida Lake as a stop-over location by migrating cormorants may not exactly have been a linear function of the number of birds breeding on Lake Ontario (see **Appendix I**). Therefore, using the same nesting population data we also fit a logarithmic function, representing a greater use of Oneida Lake by non-resident birds in early years. The resulting logarithmic model: $\ln(y) = 282(\ln(x)) - 1470$ ($R^2 = 0.89$) does fit the 1987 observation, and provides estimates for the late 1980s and early 1990s that correspond with unpublished reports and limited anecdotal information, but likely over-estimates abundance in the early 1980s. Both of these models are derived from actual population parameters from the region, and both are included to provide upper and lower estimates for inference regarding the historic use of Oneida Lake by migrating cormorants, since empirical population data are not available. Because cormorant abundance is not constant during the migration period, we calculated average weekly abundance for August through September, 1995-1997, and used the ratio of the annual peak number of migrants to the average weekly migrant population (0.44) to estimate weekly cormorant abundance from the model output.

Time in residence on the lake varies for all three cormorant groups, and relative duration was accommodated in the consumption model. For years prior to 1995, breeding adults (twice the peak nest count) were allocated 190 d in residence

(10 April-15 October), juveniles assigned 125 d (15 June-15 October), and migrants (the number of birds in excess of the number of adults and fledged juveniles) were assigned 76 d (1 August-15 October). These dates were derived from observations of annual patterns in count and breeding data collected 1995-2003 (Coleman 2009, Chapt. 2). From 1995 to 2005, we enumerated cormorant feeding days using the mean of weekly counts conducted during the migration period from 1 August to 15 October, which included resident adults, fledged juveniles, and non-resident migrants. For continuity with the previous time period, breeding adults were represented by doubling the peak nest count, and we ascribed 113 d in residence prior to 1 August (10 April-31 July).

Cormorant chicks have a lower daily food intake than adults (Fowle 1997; Richmond and Wesolowski, NYCFWRU unpublished data). We adjusted the feeding days of juvenile cormorants by a factor of 0.75/day for 56 d after hatching, reflecting the difference between juvenile daily consumption (327g; Fowle 1997) and our estimated adult consumption of 437 g day^{-1} (20% of body mass consumed per day; Dunn 1975, Glahn and Brugger 1995, Grémillet et al. 2000, Engström 2001), based on the average weight of 236 cormorants from Oneida Lake measured between 1995-2005 (2185 ± 19 g $bird^{-1}$ [mean ± 1 SE]). After 8 weeks of age, fledged cormorants were considered to recruit to the adult consumption rate (Madenjian and Gabrey 1995), thus our cormorant feeding days are in units equivalent to adult cormorant consumption. Juvenile feeding days for 1995-2005 were adjusted by 0.70/day because of the shorter time period (46 days) between 15 June and 1 August, when actual weekly counts of all birds were incorporated in the model. These methods differ slightly from those presented by VanDeValk et al. (2002) and Rudstam et al. (2004), mainly due to a lower mean body weight from our larger cormorant sample, thus our

estimates for annual consumption may be slightly different than those reported previously for Oneida Lake.

Fish abundance

For half a century, walleye and yellow perch have been monitored at all life stages in Oneida Lake using multiple gears and techniques. Numbers of adult walleye (age-4+ yr) and adult yellow perch (age-3+ yr) have been estimated periodically by mark-recapture since 1958, and adult and subadult fish are sampled annually using standardized gillnet sets and bottom trawling that date to 1957 and 1961, respectively (for details of sampling methodology see Irwin et al. 2008). Mark-recapture of adult percids was conducted through fin clipping of adults during April spawning runs, and subsequent recapture by electrofishing, gillnetting, and trawling in the summer and fall, resulting in a spring (April) population estimate. Mark-recapture analyses were routinely conducted in the 1960's and 1970's, and resumed in 1988 through the present. Different time intervals elapsed between adult walleye population estimates in the past, but since 1995, surveys were conducted every other year, and 22 years of population estimates exist between 1958 and 2005. Abundance between mark-recapture years was calculated from adjacent estimates and observed mortality rates, and by using an alternate index based on trap-net catches from 1978-1987, when mark-recapture surveys were not conducted. For yellow perch, mark-recapture efforts were more limited and more variable. Mark-recapture estimates, obtained in the 1970s, 1988, 1990, and 1995–2001, were used to derive abundance of age-3+ perch. For other years, we used an index based on gill nets catches and size-specific catchability (Forney et al. 1994).

We estimated subadult walleye (1-3 yr) abundance using age-specific catchability values for the standardized gillnet and bottom trawl sampling procedures employed at CBFS (Irwin et al. 2008). Densities for all subadult age classes were

determined using the average of density estimates from both gears. Because the catchabilities derived by Irwin et al. (2008) relate to abundance estimates from mark-recapture estimates in the spring, all walleye abundance estimates are related to the spring population. Subadult yellow perch, age-1 and to a lesser degree age-2, have low catchability in the standard gill nets. Therefore, unlike methods used for walleye, we estimated age-1 perch abundance from spring trawl data, and we back-calculated age-2 yellow perch from our estimates of age-3 perch assuming the same survival as observed between age-3 and age-4 yellow perch in Oneida Lake during the most recent mark-recapture years: 1997, 1999, and 2001 (56%, range: 43-68%).

Rudstam et al. (2004) detail the declines in percid recruitment observed in the 1989-1997 year classes, indicative of increased subadult mortality. We re-examine these recruitment relationships through 2005 (2001 walleye year class, 2002 yellow perch year class) to explore the potential impact of the cormorant management program on subadult percid mortality. We also use survival and recruitment estimates derived from the long-term data to assess the relative contributions of cormorant control and angler harvest management to recent walleye population increases by projecting adult walleye abundance from 1992 to 2015 using a simple predictive model (see results for detailed description).

For estimating cormorant selectivity, we also needed estimates of age-0 yellow perch and walleye. Age-0 fish are too small to be caught in gillnets, and since we did not recover fish smaller than 34 mm in the diet samples, we used age-0 abundance from summer trawl catch data. These trawl catches are used to derive abundance on 1 August (Mills and Forney 1988; Irwin et al. in press). A late-summer population estimate is more appropriate for this study since age-0 fish are not present in early April, and mortality of YOY fish is extremely high during the first month of life. Abundance estimates for older age groups are for spring (April).

RESULTS

Cormorant diet and selectivity

Cormorant diet samples collected from 1994-2003 (n = 137 stomach samples and n = 2375 regurgitated boluses) included 8040 individual prey specimens composed of 27 different species, and varied in composition by year and by season (Table 3.1). Yellow perch and walleye consistently comprised the majority of prey biomass in all years, accounting for 58-72% of annual diet samples by weight (Table 3.2), and together constituted 64% of the biomass recovered from all samples when summed across all 9 years. Yellow perch were also ubiquitous in the diet samples numerically, but many small forage fish were also more common in the diets by number than their contribution by weight suggests (Table 3.1). The presence and/or abundance of some species varied considerably by year, which was particularly evident for gizzard shad, white perch, emerald shiner (*Notropis atherinoides*), and freshwater drum (*Aplodinotus grunniens*), whose representation in cormorant diet reflected the abundance of strong year classes in the lake.

Analysis of selectivity by age for walleye and perch reveals considerable variation in annual exploitation, especially towards the ends of the age spectra, but E^* values averaged across the 9 years of this study depict distinct curves for both species (Fig. 3.1). Selection for walleye focuses on subadults (age 1-3), all of which display positive, and occasionally strong, selection in most years. Numerically, age-1 was the most common age in all samples at 40%, followed by age-2 at 27%. Age-0 walleye constituted 16% of all walleye in the diets, but accounted for nearly 40% of the walleye recovered after 1 August. The proportions of age-0 and age-4 walleye in cormorant diets were highly variable among years, and these age groups were not selected in most years. Walleye that reach age-5+ are rarely depredated by cormorants in Oneida Lake, and accounted for just 1.3% of all walleye in cormorant diets.

Table 3.1. Species composition and monthly distribution for double-crested cormorant prey at Oneida Lake, New York, sampled over 9 years: 1994-1996 & 1998-2003 (n = 2375 regurgitated boluses, n = 137 stomach samples). Occurrence by month is the proportion of the number of prey of each species out of the total number of individual prey items collected in each month across all years. The range of total annual diet represents the minimum and maximum proportion by weight for each species in all years sampled.

Species	No. years observed (out of 9)	Number by month (%)							Range in percent of total annual diet by weight (%)
		Apr*	May	Jun	Jul	Aug	Sep	Oct*	
Yellow perch *Perca flavescens*	9	58.8	39.0	56.3	59.1	48.4	32.6	29.4	16.6 - 50.6
Walleye *Sander vitreus*	9	11.8	1.7	11.6	10.2	7.1	2.0	3.4	19.2 - 41.2
Pumpkinseed/Bluegill *Lepomis spp.*	9	23.5	4.5	6.0	5.4	4.7	0.9	0.6	1.6 - 18.9
White sucker *Catostomus commersonii*	9	0	1.7	0.7	0.5	0.3	0	0	1.5 - 19.4
Burbot *Lota lota*	9	5.9	1.1	1.6	1.9	0.6	0.1	0.3	0.6 - 16.8
Logperch *Percina caprodes*	9	0	0	4.7	16.9	7.3	5.6	16.6	0.1 - 7.9
Smallmouth bass *Micropterus dolomieui*	9	0	2.8	1.6	1.0	1.3	0.6	2.6	1.0 - 4.3
Rock bass *Ambloplites rupestris*	9	0	0.6	2.0	0.9	1.2	0	0	0.5 - 2.7
White perch *Morone americana*	8	0	5.1	1.8	0.2	0	0.2	0.9	0 - 14.4
Emerald shiner *Notropis atherinoides*	8	0	4.0	9.9	1.1	5.4	43.2	36.3	0 - 2.3
Gizzard shad *Dorosoma cepedianum*	6	0	0	2.0	1.8	22.3	12.2	1.7	0 - 3.3
Common mudpuppy *Necturus maculosus*	5	0	0	0.5	0.4	0	0	0	0 - 2.1
White bass *Morone chrysops*	5	0	0	0.2	<0.1	0	1.8	4.0	0 - 1.9
Tesselated darter *Etheostoma olmstedi*	4	0	6.2	0.2	<0.1	0.8	0.3	3.4	0 - 0.1
Pike/Pickerel *Esox spp.*	4	0	0	0.2	0.1	0	0	0	0 - 2.8
Black crappie *Pomoxis nigromaculatus*	3	0	0	<0.1	<0.1	0	0	0.3	0 - 0.3
Largemouth bass *Micropterus salmoides*	3	0	0	<0.1	0.1	0.3	0.2	0.3	0 - 0.1
Banded killifish *Fundulus diaphanus*	3	0	0	0.2	0	0.3	0.1	0	0 - <0.1
Freshwater drum *Aplodinotus grunniens*	2	0	0	<0.1	0.2	0.1	0	0	0 - 7.8
Channel catfish *Ictalurus punctatus*	2	0	0	0.1	<0.1	0	0	0.3	0 - 1.7
Brown bullhead *Ameiurus nebulosus*	2	0	0	0.2	0	0	0	0	0 - 1.3
Trout-perch *Percopsis omiscomaycus*	2	0	33.3	0.3	0	0	0.1	0	0 - 0.4
Crayfish family Cambaridae	1	0	0	0	<0.1	0	0	0	0 - <0.1
Fallfish *Semotilus corporalis*	1	0	0	<0.1	0	0	0	0	0 - <0.1
Bowfin *Amia calva*	1	0	0	<0.1	0	0	0	0	0 - <0.1
Total no. prey sampled by month:		17	177	2630	3157	779	930	350	sum: 8040

* April samples collected in 1996 only, October samples collected in 1995 and 1996

Table 3.2. Total annual consumption by weight for double-crested cormorants on Oneida Lake, New York, relative annual percid composition in diets, and estimated impact on most vulnerable ages of yellow perch and walleye relative to their total biomass in springtime (approx. 1 May)

	Total annual consumption (kg)		No. diet	Composition by weight (%)			Proportion of biomass consumed[2] (%)		
Year	Linear model	Log model	samples[1]	Yellow perch	Walleye	Total percid	Yellow perch	Walleye	Total percid
1986	5,365	14,132	-	-	-	-	0.5 - 1.3	1.4 - 3.6	0.7 - 1.8
1987	10,544	19,338	-	-	-	-	1.1 - 2.0	1.1 - 2.0	1.1 - 2.0
1988	13,779	22,362	-	-	-	-	1.8 - 2.9	1.1 - 1.9	1.4 - 2.3
1989	18,965	26,362	-	-	-	-	2.4 - 3.3	2.3 - 3.3	2.4 - 3.3
1990	24,982	31,778	-	-	-	-	3.8 - 4.8	1.8 - 2.3	2.6 - 3.3
1991	35,238	39,714	-	-	-	-	6.1 - 6.9	3.2 - 3.6	4.4 - 5.0
1992	38,781	42,962	-	-	-	-	4.2 - 4.7	7.2 - 8.0	5.1 - 5.7
1993	49,350	51,896	-	-	-	-	6.9 - 7.3	13.4 - 14.1	8.7 - 9.2
1994	34,363	38,458	296[3]	31.7	21.9	53.6	9.0 - 10.0	4.0 - 4.5	5.9 - 6.6
1995	46,302		518	33.5	24.2	57.7	7.2	11.5	8.6
1996	72,310		658	50.6	21.5	72.1	15.4	30.9	18.1
1997[4]	79,552		138	73.4	3.4	76.8	30.8	4.2	24.1
1998	56,128		50	43.6	19.2	62.8	15.2	12.7	14.3
1999	54,668		188	45.0	26.0	71.0	10.4	23.1	13.0
2000	54,922		189	42.2	29.7	72.0	14.2	14.7	14.4
2001	50,279		225	38.6	31.7	70.3	10.7	11.3	11.0
2002	45,531		257	31.0	28.5	59.5	3.2	6.7	4.3
2003	39,084		131	16.6	41.2	57.9	2.7	18.0	6.8
2004	21,188		-	-	-	-	4.2	2.7	3.4
2005	13,642		-	-	-	-	2.7	5.2	3.4

Notes: Consumption is derived from weekly counts of adults and chicks, estimates of migrant populations in the 1980s and early 1990s, and daily food intake equaling 20% of mean body mass (adult: 437 g day^{-1}, chick: 327 g day^{-1} to 56 d, then adult rate). Migrant populations were estimated from the number of nesting adults on Lake Ontario using 2 different models, linear and logarithmic regression, resulting in different estimates for total annual consumption through 1994. Percid biomass is derived from spring population estimates for age 1-6 yellow perch and age 1-4 walleye, annual mean lengths by age in spring (back-calculated from summer lengths), and length-weight regressions derived at Oneida Lake (young-of-year fish were not included in biomass estimate). The 2 values for proportion of biomass consumed represent estimates from the 2 population models (linear and logarithmic).

[1] Sample unit = entire regurgitated food bolus or individual stomach with contents

[2] Mean diet composition used to calculate annual consumption when diet data not available (37.0% yellow perch, 27.1% walleye)

[3] Sample size estimated from known no. of total prey and mean no. fish per sample in 1995 and 1996

[4] Diet analysis conducted by alternate method (pellets) in 1997, see VanDeValk et al. 2002

Cormorants exploit a wider range of yellow perch age groups, and there is considerable annual variability in electivity coefficients. Average electivities show a consistent pattern of selection for age 2- 4 perch, however, over other age groups (Fig. 3.1). As found with walleye, age-1 was the most common age recovered, and constituted 56% of all perch in the diets, followed by age-0 at 20% and age-2 at 11%. Older perch, ranging from age 6-8, were present but not common and accounted for 1% of all perch in the diets. Of the perch recovered after 1 August, age-0 accounted for 63% by number.

A plot of mean electivity by age class for walleye and perch against mean length-at-age for fish caught in gillnets in May – July, 1994-2003 (n = 1025 walleye, n = 3040 yellow perch), shows that cormorants select longer walleye than yellow perch (Fig. 3.2A). To investigate if this could be due to the larger girth of yellow perch at a given length, we also plotted mean electivity by age as a function of fish girth based on average length-at-age and length-girth relationships derived from Oneida Lake gillnet catches in 1994. This revealed almost identical curves for the indices of both species, peaking around a girth of 150 mm (Fig. 3.2B).

Cormorant control and impact on consumption

The cormorant management program effectively interrupted the annual growth of the breeding population on Oneida Lake, decreased the reproductive output of the colony, and rapidly moved migrating cormorants off the lake each fall (Coleman 2009, Chapt. 2). As a direct result, the annual consumptive impact of cormorants on the system was reduced by approximately 30% of the 1997 level in the first year (1998), and declined by 83% of the 1997 level by 2005 (Fig. 3.3, Table 3.2). These reductions equate to an estimated decrease of 23,400 – 65,900 kg of all prey consumed per annum over the 8 years of the management program. Changes in total annual

Figure 3.1. Relativized electivity indeces (E^*) for double-crested cormorants feeding on multiple age classes of walleye and yellow perch in Oneida Lake, New York. Only summer diet samples, May-July, were used for selectivity analysis since these data were uniformly available for most years of the study. The electivity coefficient E^* is defined between -1 and +1, with neutral electivity indicated by a zero value. Mean annual electivities are represented by the large black circles, and error bars are ± 1 SD.

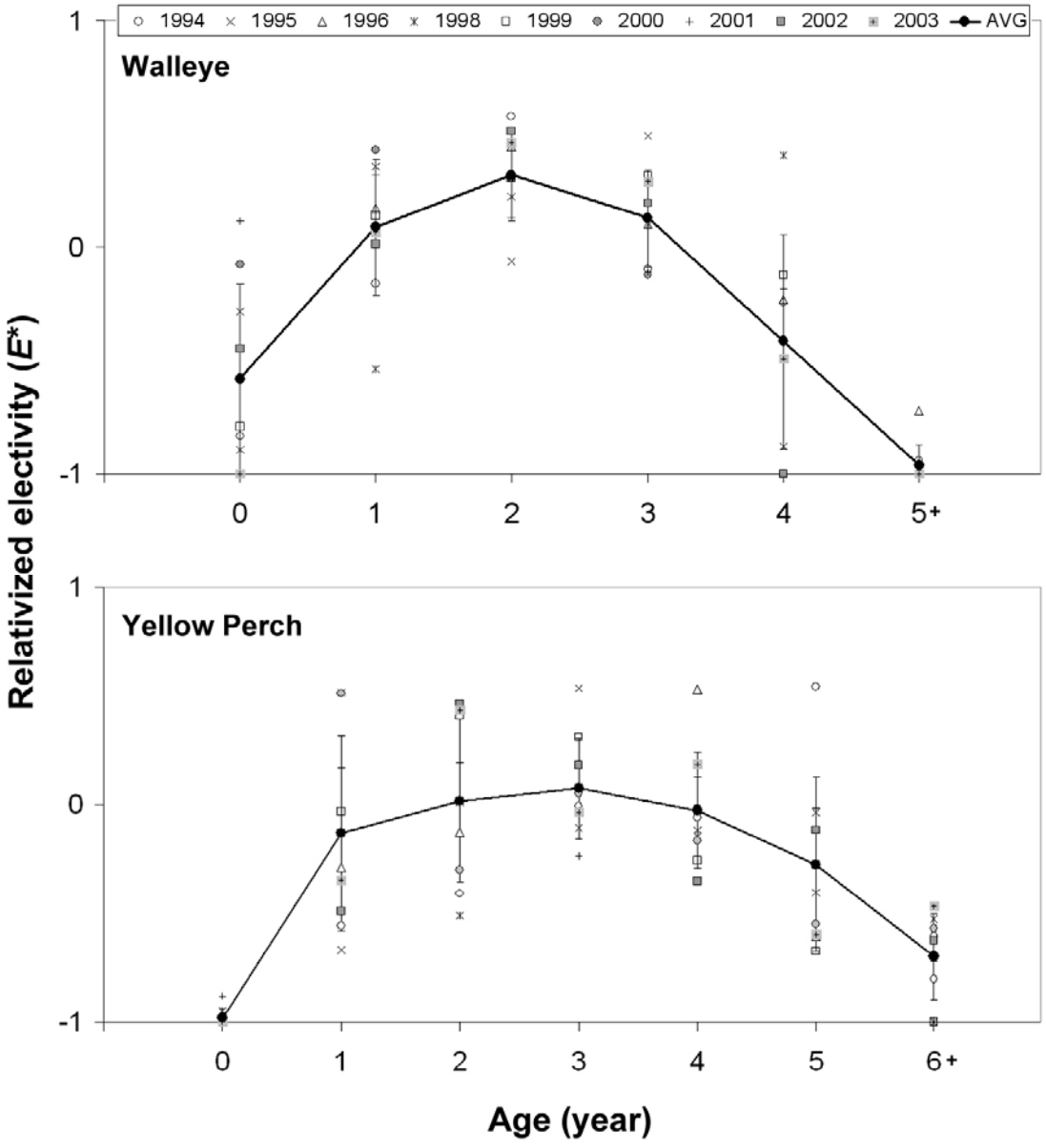

1994
1995
1996
1998
1999
2000
2001
2002
2003
AVG
Walleye
Yellow Perch
Relativized electivity (E*)
Age (year)
1
0
-1
0
1
2
3
4
5+
5
6+

Figure 3.2. Mean relativized electivities by age class plotted against: **A)** the mean total length at age for fish caught in gillnets in May – July, 1994-2003 (n = 1025 walleye, n = 3040 yellow perch), error bars are ± 1 SD. **B)** the girth (maximum circumference with fins compressed) estimated for the mean length of each age class. The length-girth relationships depicted were derived from fish caught in gillnets set in Oneida Lake in 1994 (n = 48 walleye, n = 160 yellow perch). Ages of fish increase from left to right, starting with age-0, and correspond with the ages presented in Figure 3.1 (age-0 to 5+ for walleye, age-0 to 6+ for yellow perch).

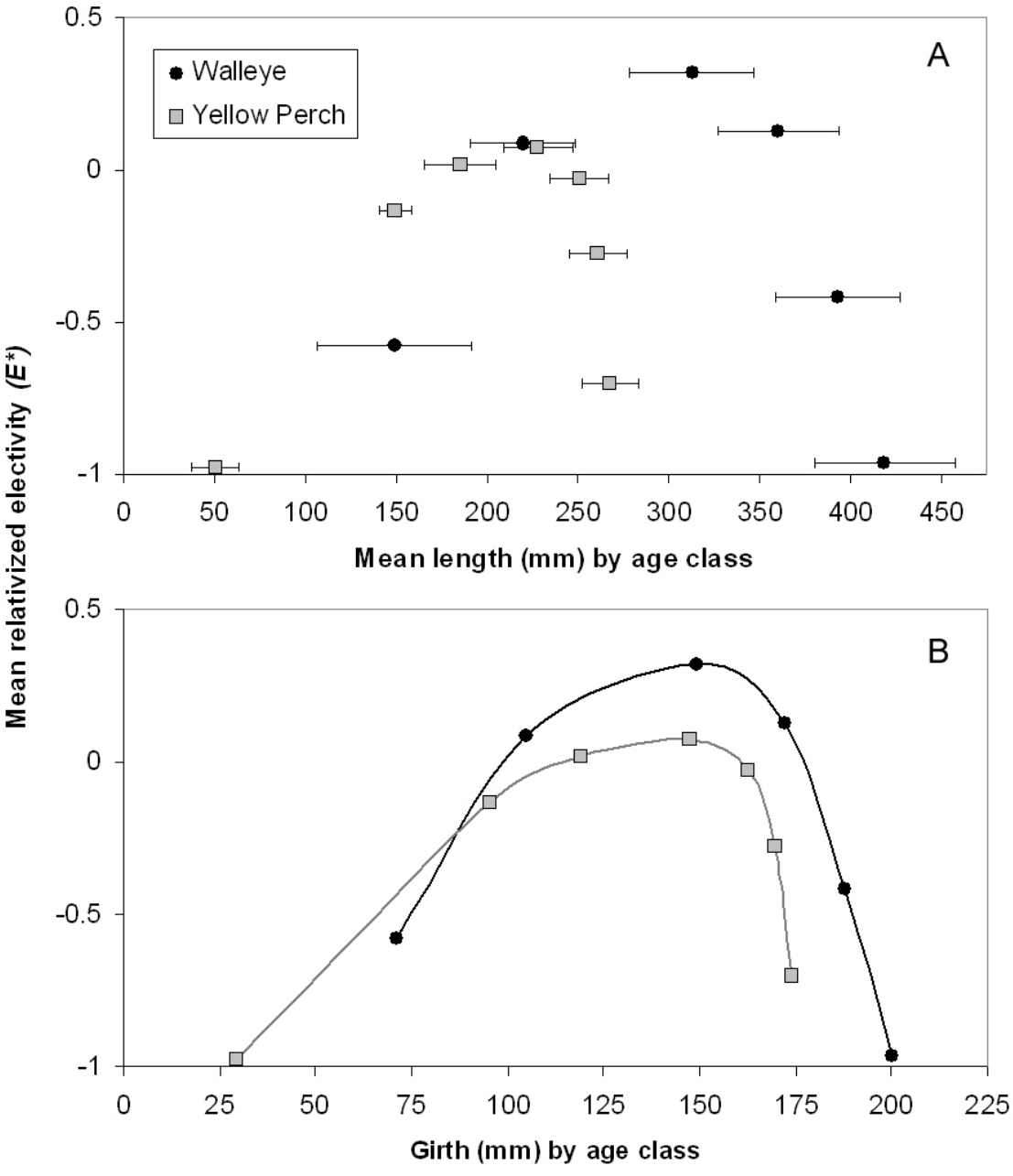
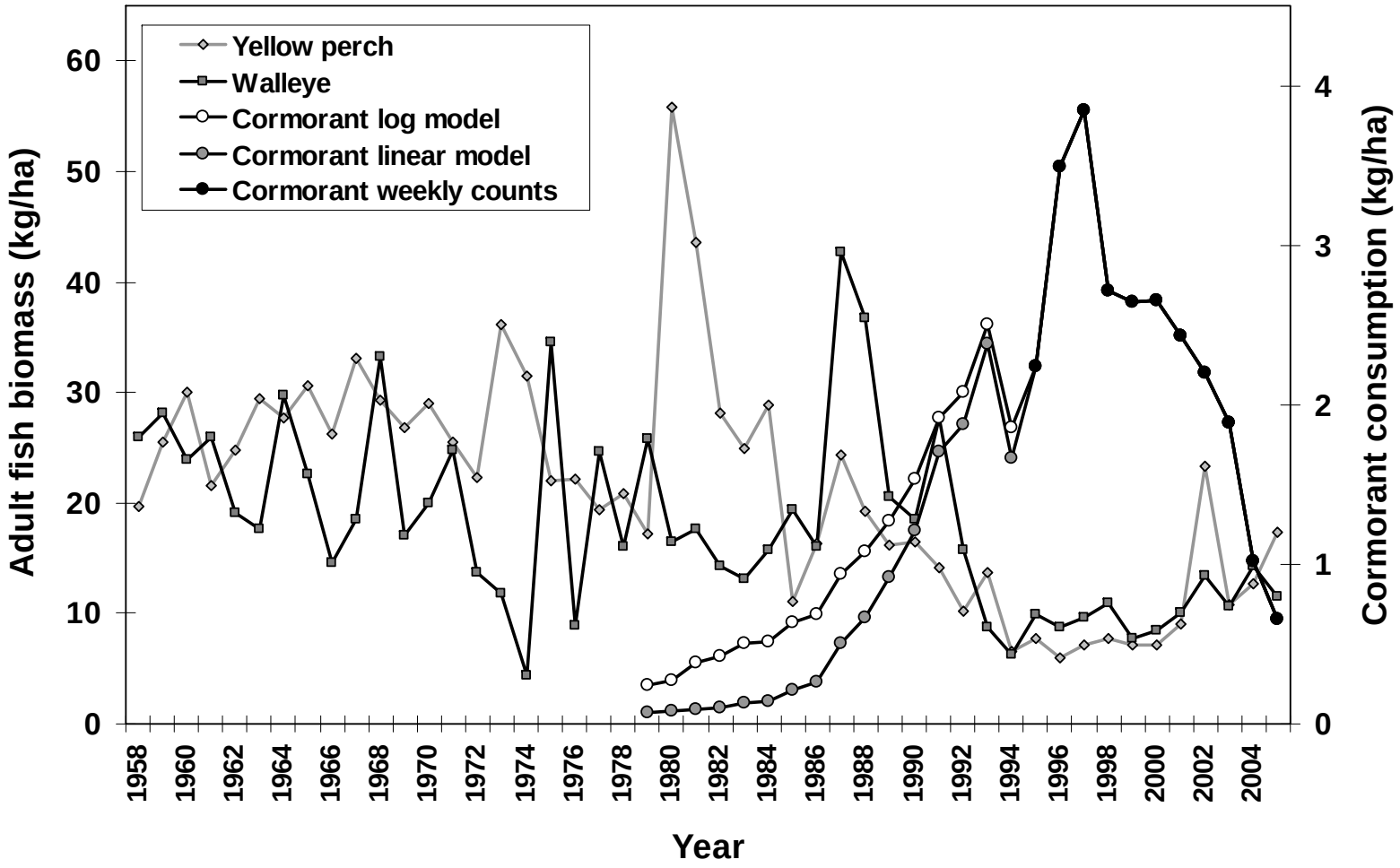

A
Walleye
Yellow Perch
0.5
0
-0.5
-1
0
50
100
150
200
250
300
350
400
450
Mean relativized electivity (E*)
Mean length (mm) by age class
B
0.5
0
-0.5
-1
0
25
50
75
100
125
150
175
200
225
Girth (mm) by age class

Figure 3.3. Annual biomass estimates for adult walleye (age-4+ yr) and adult yellow perch (age- 3+ yr) from 1958 to 2005, and the estimated total annual consumption per area for double-crested cormorants on Oneida Lake, New York, from 1978 to 2005. Percid biomass is derived from spring population estimates for yellow perch and walleye, annual mean lengths by age in spring (back-calculated from summer lengths), and length-weight regressions derived at Oneida Lake. Two different models were used to estimate the migrant cormorant population on Oneida Lake from 1979-1994 because comprehensive counts were not available (see Appendix I). Because each of the models fit the existing count data better at different periods, both were included to represent upper and lower estimates for consumption.


Yellow perch
Walleye
Cormorant log model
Cormorant linear model
Cormorant weekly counts
Adult fish biomass (kg/ha)
Cormorant consumption (kg/ha)
Year
0
10
20
30
40
50
60
0
1
2
3
4
1958
1960
1962
1964
1966
1968
1970
1972
1974
1976
1978
1980
1982
1984
1986
1988
1990
1992
1994
1996
1998
2000
2002
2004

consumption based on cormorant feeding days do not necessarily equate directly to commensurate impacts on walleye and yellow perch, however, because species composition of cormorant diet varies among years. If we account for annual percid abundance and representation in cormorant diet samples, we estimate that cormorants consumed approximately 24% of the total spring biomass for age 1-4 walleye and 1-6 yellow perch in 1997, the peak year (Table 3.2; age-0 fish were included in annual consumption calculation but were not included in estimates of biomass consumed due to the huge intra-annual variability inherent in such estimates). The proportion of the total percid biomass consumed annually by cormorants has declined since 1997, however, cormorants still consumed over 10% of spring biomass through 2001, which is higher than estimated consumption in the late 1980s and early 1990s. Considered separately, estimated consumption of perch and walleye also indicates a protracted period of relatively high levels of predation, equaling or exceeding the annual estimates from the higher logarithmic population model for the early and mid-1990s (Table 3.2).

Fish population dynamics

The deviation from the historic relationship between age-1 and age-4 walleye presented by Rudstam et al. (2004) was first evident in the early 1990s. Starting with the 1989 year class, the predictive recruitment model repeatedly over-estimated the number of adult walleye to recruit at age-4, indicative of increased mortality of subadult fish (Fig. 3.4, see also Rudstam et al. 2004). Year classes from 1989 to 1996 contributed an average of 49,400 age-4 walleye (range: 8,400-144,000) to the adult population, despite an average expected contribution of 108,000 fish (range: 44,800-295,400) (Fig. 3.5). The 1997 walleye year class was the first to experience reduced predation during ages 1-3 resulting from cormorant management, and was also the first year class in several years to exceed the number predicted to recruit in 2001

(77,730 predicted, 80,700 observed). Subsequently, annual recruitment of walleye through 2005 returned to levels expected given the number of age-1 fish caught in summer trawls (Fig. 3.4). Between 2001 and 2005, an average of 96,000 walleye recruited to the adult population annually (range: 57,500-127,400), contributing to an average annual increase to the adult population of 14% $year^{-1}$ from a low of 215,600 adult walleye in 1999. The mean number of walleye expected to recruit over the same 5 years was 77,000 $year^{-1}$ (range: 55,200-106,400).

The relationship between predicted and observed recruitment for yellow perch is more variable than it is for walleye. A similar pattern of over-predicting annual recruitment to adult stock also exists for perch, dating to the late 1980s. Unlike walleye, however, we have not observed a return to predicted recruitment values for yellow perch in recent years (Fig. 3.4). During the 1990s and 2000s, there have been several strong year classes to survive the first winter that have not contributed reciprocal numbers to the adult stock (Fig. 3.6). Despite lower than expected recruitment, and a continuing trend towards lower annual recruitment, survivors from strong years have gradually helped to increase the total adult yellow perch population by approximately 20% $year^{-1}$, growing from an historic low of 561,000 fish in 1996 to over 1.5 million perch in 2005.

Impact of harvest management

A simple modeling exercise, based on empirical population data, was used to elucidate the contribution of angler harvest management to the increasing adult walleye population evident from 2001-2005 (Fig. 3.7). We explored five scenarios, three of which model both cormorant and angling mortality from 1992 through 2000 as observed: survival (S) = 0.75 ($\overline{x}$: 1964-2000, SE = 0.04), and annual recruitment (R) = 39,390 fish ($\overline{x}$: 1992-2000, SE = 13,800). Scenario 1 projects walleye population growth to 2015 as if no cormorant or harvest management had been

instituted. Assuming mortality and cormorant impact on recruitment were constant, this scenario results in an adult walleye population of approximately 158,000, less than ¼ the long term average of 670,900 ± 34,000 (mean ± 1 SE) from 1957-1991. Starting with 2001, the first year in which a walleye year class recruited to the adult population under levels of predation pressure tempered by cormorant control in all subadult years (ages 1-3), we explored two scenarios simulating the changing survivorship we observed, both using the mean recruitment predicted at age-4 from abundance at age-1: R = 115,000 fish ($\overline{x}$: 1993-2005, SE = 17,200). Scenario 2 maintains the average survival rate observed from 1964 to 2000 (S = 0.75), representative of maintaining the 380 mm size limit. Scenario 3 incorporates the increased adult survival observed from 2001 to 2005 (S = 0.83, SE = 0.05) presumably resulting from the 457 mm size limit, then reverts back to S = 0.75 in 2006 when the size limit was changed back to 380 mm. Both scenarios, 2 and 3, level out at a population of approximately 460,000 walleye in 2015, but Scenario 3 does provide for more rapid growth in the population, differing by as much as 90,000 fish in 2005. For comparison purposes, the last two are hypothetical scenarios that model walleye population as if cormorants had disappeared from the lake after 1992. Scenario 4 projects population growth using the annual number of adult walleye predicted to recruit between 1993 and 2005, then the mean from 2006 onwards (R = variable 1993-2005 [range: 45,000-385,000], then R = 115,000 [$\overline{x}$: 1993-2005]) with the long-term mean survival (S = 0.75), resulting in an adult population of 420,000 fish in 2015. Lastly, Scenario 5 adds the simulated closure of the fishery to angling starting in 1993, and we used 10% estimated natural mortality (S = 0.90, see Irwin et al. 2008) and R = 115,000 fish to produce a hypothetical adult population of 1,100,000 walleye in 2015. This value exceeds the maximum walleye population for Oneida Lake, recorded in 1958, by approximately 60,000 fish.

Figure 3.4. The relationship between the number of fish predicted to recruit to the fishery at age-4 (walleye) and age-3 (yellow perch), based on catches at age-1 in standardized trawls, and the number estimated (observed) to recruit 3 and 2 years later, respectively. The dotted line at 1 represents a precisely accurate prediction.

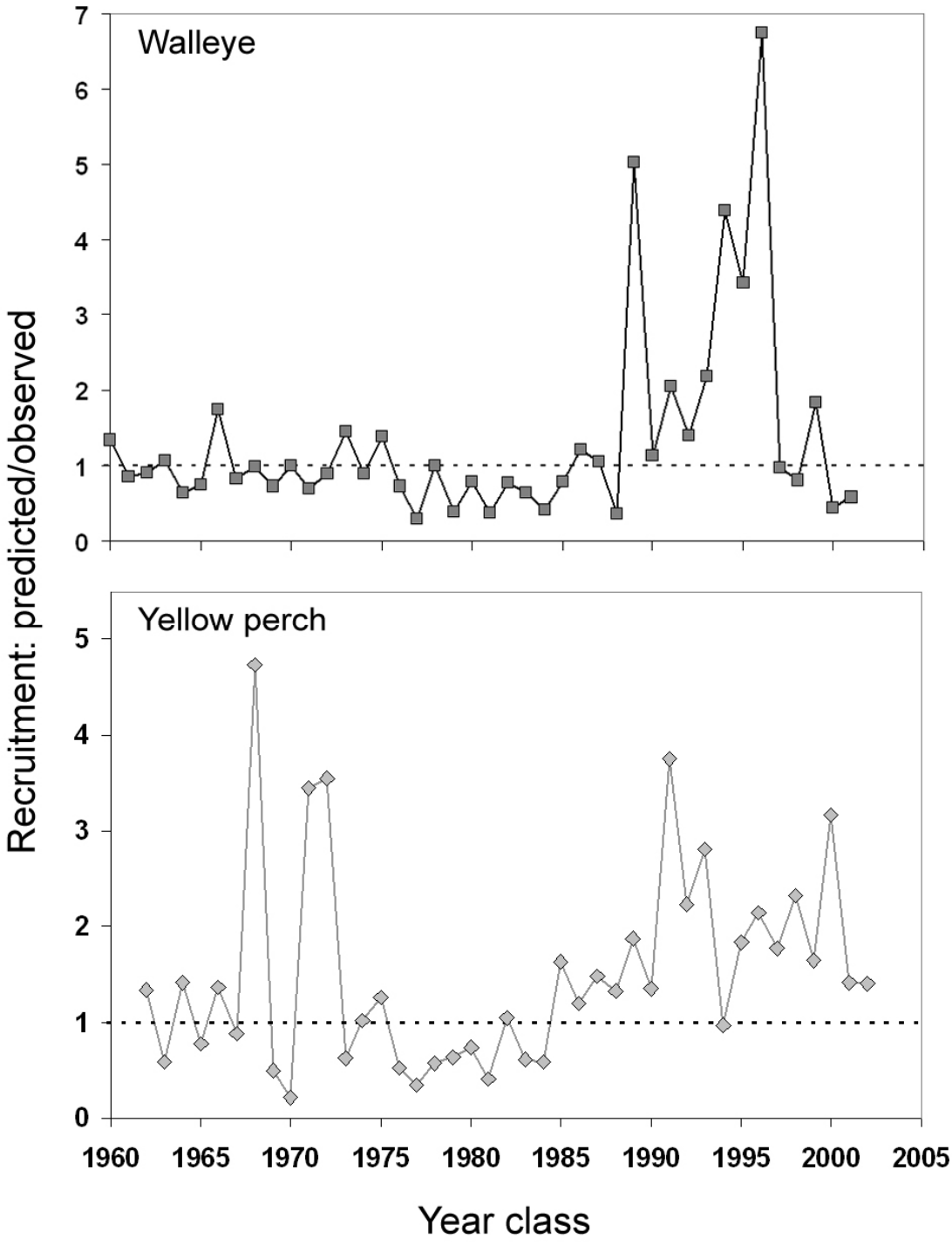

Walleye
Yellow perch
Recruitment: predicted/observed
Year class
0
1
2
3
4
5
6
7
1960
1965
1970
1975
1980
1985
1990
1995
2000
2005

Figure 3.5. Estimates of walleye abundance for year classes from 1961-2004 at Oneida Lake. Age-1 CPUE represents mean catch-per-unit-effort in standardized bottom trawls conducted from July-October. Estimates for ages 4 and 5 are based on mark-recapture studies conducted in 22 non-consecutive years between 1958 and 2005, with years between mark-recapture efforts calculated from adjacent estimates and observed mortality rates. An alternate index was used between 1978 and 1987, based on trap-net catches because mark-recapture surveys were not conducted (for more details, see: Forney 1980; Rudstam et al. 2004; Irwin et al. 2008).

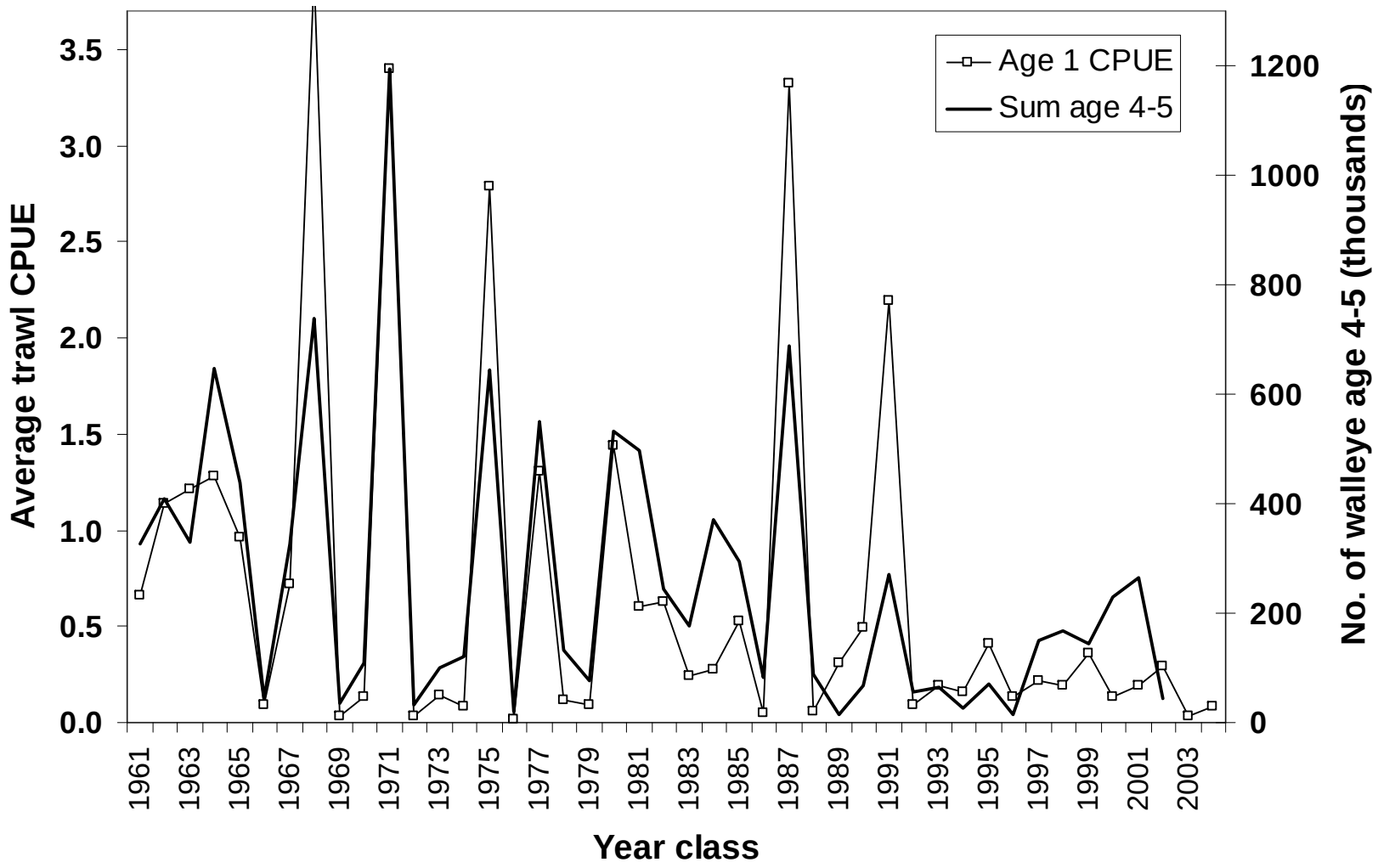
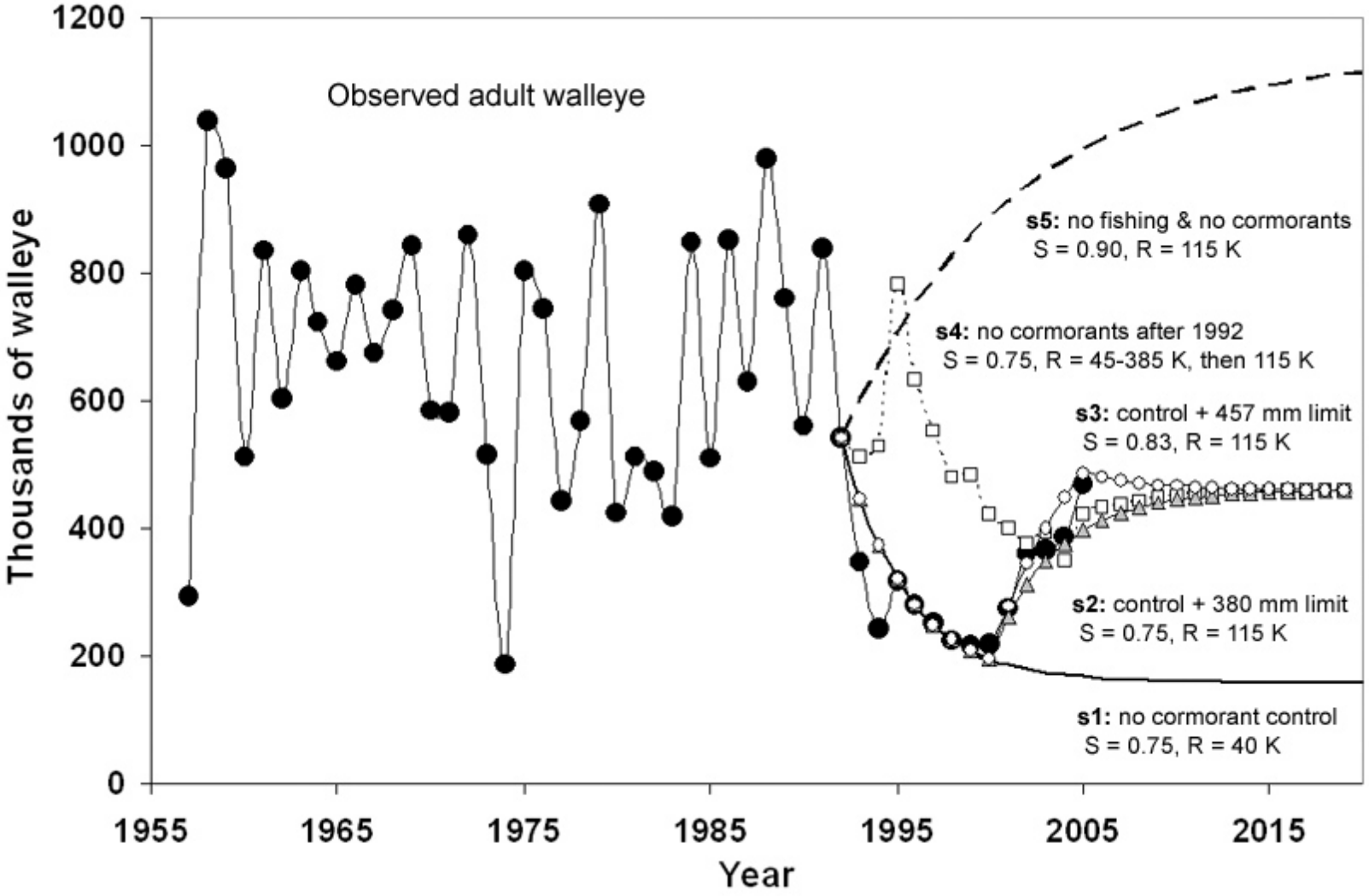

Age 1 CPUE
Sum age 4-5
Average trawl CPUE
No. of walleye age 4-5 (thousands)
Year class
0.0
0.5
1.0
1.5
2.0
2.5
3.0
3.5
0
200
400
600
800
1000
1200
1961
1963
1965
1967
1969
1971
1973
1975
1977
1979
1981
1983
1985
1987
1989
1991
1993
1995
1997
1999
2001
2003

Figure 3.6. Estimates of yellow perch abundance for year classes from 1961-2004 at Oneida Lake. Age-1 estimates are based on mean CPUE in bottom trawls conducted around 1 May (spring) and from July-October (summer). Estimates for ages 3-5 are based on mark-recapture studies conducted between 1958 and 2005, with years between mark-recapture efforts calculated from adjacent estimates and observed mortality rates. An alternate index based on gillnet catch was used for estimates in years when mark-recapture surveys were not conducted, and estimates could not be extrapolated from mark-recapture.

Sum age 3-5
Age 1 Spring
Age 1 Summer
No. yellow perch age 3-5 (thousands)
No. yellow perch age 1 (thousands)
Year class
0
2,000
4,000
6,000
8,000
10,000
12,000
14,000
16,000
18,000
1961
1963
1965
1967
1969
1971
1973
1975
1977
1979
1981
1983
1985
1987
1989
1991
1993
1995
1997
1999
2001
2003

Figure 3.7. Historic adult walleye abundance for Oneida Lake, New York, and 5 predictive modeling scenarios based on the 1992 population level and various recruitment (R) and survival rate (S) simulations associated with cormorant management. Three of the 5 scenarios model cormorant and angling mortality from 1992 through 2000 as observed (S = 0.75, R = 40,000 fish). Scenario 1 (**s1**) projects walleye population growth to 2015 as if no cormorant or harvest management had been instituted. Starting in 2001, the first year in which a walleye year class recruited to the adult population with the influence of cormorant control in all subadult years (ages 1-3), we explored two scenarios simulating the changing recruitment levels, both using R = 115,000 fish, the mean predicted recruitment from 1993-2005. Scenario 2 (**s2**) maintains the average survival rate observed from 1964 to 2000 (S = 0.75), representative of maintaining the 380 mm size limit. Scenario 3 (**s3**) incorporates the increased adult survival observed from 2001 to 2005 (S = 0.83) resulting from the 457 mm size limit, then reverts back to S = 0.75 in 2006 when the size limit was changed back to 380 mm. The last two are hypothetical scenarios that model walleye population as if cormorants had disappeared from the lake after 1992. Scenario 4 (**s4**) projects population growth using the annual number of adult walleye predicted to recruit between 1993 and 2005 (R = variable 1993-2005 [range: 45,000-385,000], then R = 115,000 [$\overline{x}$: 1993-2005]), with the long-term mean survival (S = 0.75). Scenario 5 (**s5**) adds the simulated closure of the fishery to angling starting in 1993, and we used 10% estimated natural mortality (S = 0.90, see Irwin 2006) and R = 115,000 fish.


Observed adult walleye
Thousands of walleye
Year
1200
1000
800
600
400
200
0
1955
1965
1975
1985
1995
2005
2015
s5: no fishing & no cormorants
S = 0.90, R = 115 K
s4: no cormorants after 1992
S = 0.75, R = 45-385 K, then 115 K
s3: control + 457 mm limit
S = 0.83, R = 115 K
s2: control + 380 mm limit
S = 0.75, R = 115 K
s1: no cormorant control
S = 0.75, R = 40 K

DISCUSSION

Cormorant diet and selectivity

The diet of resident and transient double-crested cormorants on Oneida Lake consists of a diverse array of species, suggestive of a generalist feeding habit. Annual variation in species composition did reflect changing prey assemblages (unpublished data), and the occurrence of species like freshwater drum, gizzard shad, and white perch, which have demonstrated more stochastic population dynamics, corresponded with changing abundance in the system (VanDeValk et al. 2006). While we have thorough population data for some of the fish species in Oneida Lake, we lack reliable population estimates for many of the smaller and/or less abundant species consumed by cormorants, which precludes a rigorous analysis of selection by species. Yellow perch and walleye, however, consistently comprised the majority of cormorant prey biomass in all years studied, and have likewise been the dominant species collected in annual gillnet sampling efforts throughout most of the time series. No age-0 fish, of any species, was found in diet samples prior to July, indicating a shorter window of time for cormorants to take advantage of an abundant food resource prior to migration. Coleman et al. (2005) speculated that the growth of age-0 fish to sizes exploitable by cormorants at Oneida Lake may have explained the lack of a "halo" effect around the nesting islands in 1999 and 2000, whereby high foraging density reduces prey abundance closest to waterbird breeding colonies, necessitating greater distances to foraging locations (Ashmole 1963, Birt et al. 1987). While we cannot validate this supposition, the shift in diet to incorporate age-0 fish that we observed, especially to gizzard shad and yellow perch in years when they were abundant (Table 3.1; CBFS unpublished cormorant diet data 1988-1991) was potentially strong enough to serve as a buffer for other species/age classes. Strong year classes of gizzard shad have been found to buffer YOY yellow perch from walleye predation in Oneida Lake, with

implications to increasing winter survival to the first spring (Fitzgerald et al. 2006). It is likely that the buffering effects of alternate forage on predation by piscivorous fish would apply to predation by avian pursuit-predators as well (Stickley et al. 1992, Glahn et al. 1995).

Like many predators in freshwater systems, cormorants swallow their prey whole; thus, gape size limits the size of fish they are able to ingest. For percids in Oneida Lake, gape size appears to confine the impact of cormorant predation primarily to age 0-4 walleye and age 0-6 yellow perch. Although the total length of walleye and perch can differ by as much as 200 mm at the upper end of these age ranges, the girth of these 2 species is essentially equivalent at the ages displaying the strongest selective preference (i.e., age-2 walleye and age-3 perch). These results indicate that cormorants are selecting the largest perch and walleye they can physically ingest, with the optimal size of approximately 150 mm. Because we examined only fish that had successfully been consumed, our data do not address questions surrounding failed ingestion attempts, and resulting injury to fish, which may be associated with girth and gape limitation (see Grémillet et al. 2006). The few observations of fish injured, but not consumed, by foraging cormorants on Oneida Lake involved walleye (n = 3) and white sucker (*Catostomus commersonii*) (n = 3) with a mean total length of ~ 400 mm (J. Coleman, personal observation, 2 August 2003). These fish were within the maximum lengths recovered in our diet samples (max. walleye = 419 mm, max. white sucker = 416 mm), but kleptoparasitism by opportunistic gulls following a large feeding flock may have interfered with attempted ingestion of the large fish due to increased handling time.

Yellow perch and walleye have a relatively narrow fusiform body type, but fish with laterally compressed morphology or protruding defensive structures have elements that add to the traditional metric for girth. Spines and barbs complicate prey

handling and ingestion, and have been implicated in prey preference of both piscivorous birds and fish (Forbes 1989, Knight and Vondracek 1993, Werner et al. 2001, Bosher et al. 2006), and in dietary differences by sex in wintering cormorants at aquaculture facilities and southern reservoirs (Stickley et al. 1992, Campo et al. 1993, Glahn et al. 1995, Fenech et al. 2004). This may account for the scarcity of ictalurids (catfish and bullhead) in our diet samples, despite the frequent occurrence of several other demersal species, such as: white sucker, burbot (*Lota lota*), logperch (*Percina caprodes*), tessellated darter (*Etheostoma olmstedi*), and mudpuppy (*Necturus maculosus*) (Table 3.1). White perch is also under-represented in Oneida Lake cormorant diet samples given the relative abundance of the species. Following a resurgence in the mid-1990s, the number of white perch exceeded walleye in annual gillnet samples collected in 2005, and the white perch has become one of the dominant species in Oneida Lake (VanDeValk et al. 2006). Larger body depth is an adaptation that has been found to reduce the risk of predation in fishes (Webb 1986, Brönmark and Miner 1992), and the deep body of white perch, coupled with stout spines in the dorsal, anal, and ventral fins, likely allow this species to outgrow cormorant predation after age-4, the oldest age class we recovered in diet samples. However, their relatively low representation in diets across all ages (age 0-4) suggests there may be other preferential factors, like handling time or spatial segregation, governing their selection. Given the propensity for predation to affect the structure of fish communities (McQueen et al. 1986, Mills and Forney 1988, Robinson and Tonn 1989, Knight and Vondracek 1992), it is possible that preferential predation on yellow perch and walleye by cormorants in Oneida Lake has contributed to the increasing white perch population by reducing competition for food resources (Prout et al. 1990), while also reducing the risk of predation from the top fish predator. Also, the white perch is

not valued as a game fish or pan-fish in central New York (personal observation), so harvest pressures exerted by local anglers are likely reduced compared to percids.

Impact of management on consumption

The management program initiated in 1998 on Oneida Lake succeeded in diminishing the predation pressures exerted by cormorants on all prey species by reducing the fecundity of the breeding colony and moving resident and non-resident birds off of the lake in the migration period (Coleman 2009, Chapt. 2). Based on the evidence assembled by Rudstam et al. (2004), we hypothesized that any such reductions would result in increased survival from age-1 to the adult stage, and a subsequent increase in adult populations in the lake. Both yellow perch and walleye adult populations reached their lowest levels around the time the management program began, in 1996 and 1999 respectively, after which both species began to exhibit steady increases in both number and biomass. Likewise, our recruitment analysis indicated that survival of subadult percids had generally increased during the years of the management program, and the selectivity analysis confirmed that these were the ages of perch and walleye selected by cormorants. Once again the timing of these observations coincided with changing cormorant populations on Oneida Lake. However, in addition to results that correspond well with the evidence presented by Rudstam et al. (2004), we have also observed some inconsistencies as well.

Cormorant diet analysis revealed that the relative composition of percids in cormorant diet did not vary appreciably from 1994-2003, and cormorants continued to consume a substantial proportion of standing perch and walleye biomass due to the decreasing abundance of those species in the system. The results of the consumptive model indicate that the relative impacts to perch and walleye remained elevated from 1999-2001, especially in relation to the period in the early 1990s when cormorant

consumption was previously implicated as a major factor precipitating the decline in percid populations observed at that time (Table 3.2; Rudstam et al. 2004).

Rudstam et al. (2004) quantified the loss of subadult perch and walleye to cormorants, and concluded that the impact of cormorants on percids presented the most parsimonious explanation for declines in annual recruitment in the mid to late 1990s, which, when coupled with sustained angling pressure, led to declines in adult populations. Starting with the 1989 year class, walleye recruitment was considerably lower than expected in 6 of the ensuing 8 years (Fig. 3.5), and an average of just 38,600 walleye recruited to the adult population annually between 1993 and 2000, including the marginally strong 1991 year class. An improved recruitment of cohorts from 1997-2001 was expected given reductions in cormorant consumption resulting from the control program, and the return to expected levels of recruitment during this time period (Fig. 3.4) appeared to further support both the effectiveness of the control program and the conclusions of Rudstam et al. (2004). However, under closer scrutiny it appears that the return to expected levels of recruitment from 2001-2005, including higher than expected numbers in 4 of the 5 years, may at least partly be the result of under-predicting the number projected to recruit due to low catches of age-1 fish in summer trawls. An assessment of year class abundance estimates for the long-term time series (Fig. 3.5) reveals a deviation in the relative abundance of age-1 and adult age classes, starting with the 1997 cohort. A number of possible explanations exist for potential changes in trawl catchability, including: increasing water clarity affecting spatial distributions of fish (Idrisi et al. 2001, Zhu et al. 2006) and catchability (see Irwin et al. 2008), weather related stratification and deoxygenation events, changes in prey composition to more pelagic species, increasing water clarity affecting gear avoidance by target fishes, and/or normal sampling variability. Therefore, at least part of the apparent recovery of walleye, and possibly yellow perch,

recruitment dynamics post-cormorant control could be due to higher number of age-1 fish than were detected by our standard trawls. Support for this comes from an increase in catches of age-2 and age-3 walleye in standard gill nets relative to catches in trawls in recent years. This apparent deviation from the long-term relationship is an important concern, and is the focus of current research by CBFS biologists. Furthermore, this potential alteration to the recruitment model raises questions about the rates of recent subadult mortality by comparison to recruitment predicted from trawl catch at age-1 after 1998. Therefore, our ability to quantitatively analyze consumption estimates and actual fish losses, as per Rudstam et al. (2004), has been compromised. From a qualitative perspective, our analysis of cormorant consumption indicates a relatively high level of impact on walleye and yellow perch persisting through 2003 that rivals estimates from 1989-1995. Increasing annual walleye recruitment to age-4, under what appears to be a high level of predation pressure, does not correspond with our expectations given previous results. Increasing adult populations of walleye and yellow perch were expected from the reduction of cormorant predation pressures, but the rate of increase we observed was more rapid than anticipated given the estimated declines in pressure.

Because the apparent inconsistency in fish population response to the estimated levels of predation pressure is based on the dramatic population declines of the mid to late 1990s, it is worthwhile to reevaluate the decline of Oneida Lake's yellow perch and walleye populations at that time, and speculate on potential contributing factors. The management of walleye populations in Oneida Lake has focused on maintaining a sustainable relationship with yellow perch, and walleye harvest regulations were developed accordingly (Forney 1980). A relatively stable state persisted through the '60s and '70s despite a long-term trend towards declining numbers of eggs, YOY, and adult yellow perch dating back to the 1960s (Hall and

Rudstam 1999, Mayer et al. 2000, Irwin et al. in press). A very strong year class of yellow perch in 1977 bolstered adult perch numbers and biomass through 1984, but annual YOY abundance dropped to low levels by the mid 1980s (Hall and Rudstam 1999, Irwin et al. in press). Rather than exhibiting a reciprocal decline, walleye productivity appeared to increase, and the 1987 cohort was one of the strongest year classes on record (Fig. 3.5). The adult population also thrived in the late '80s, and the 1988 mark-recapture study yielded an estimated 980,000 walleye, the second highest estimate since 1958 (VanDeValk et al. 2006). The divergence from the tight historic relationship between the two species is exemplified by the annual ratio of adult walleye to adult yellow perch over the past half-century. Through the 1960s and 1970s, there were approximately 3.7 adult perch for each adult walleye in the lake, but by the late 1980s that relationship dropped to 1.8 perch per walleye ($\overline{x}$: 1988-1992; Appendix II). It was during the 1980s that the abundance of alternate forage available to walleye flourished, and white perch then gizzard shad displayed periodic high production of young (Roseman et al. 1996, Fitzgerald et al. 2006). Adult walleye capitalized on these abundant resources, as evidenced by the changing proportions of prey species in fall walleye diets (Fitzgerald et al. 2006). Citing the repercussions following an irruption of gizzard shad in 1954, Mills and Forney (1988) suggested that increasing availability of gizzard shad and white perch would increase walleye production, but could also destabilize the fish community with strong intermittent year classes. While age-0 gizzard shad and white perch have not been found to negatively impact age-0 yellow perch through direct competition (Prout et al. 1990, Roseman et al. 1996), an increase in walleye abundance resulting from greater forage availability would also result in increasing mortality for YOY and age-1 yellow perch through apparent competition (Holt 1977, Polis et al. 1989, Rose et al. 1999; see Irwin 2006 and Fitzgerald et al. 2006 for a more detailed treatment). It is also likely that the same

pressures exerted on yellow perch could also result in cannibalism of age-0 walleye, especially if forage densities became low. To speculate further on the impact of alternate forage, high densities of age-0 gizzard shad may also have reduced the mortality of adult walleye by reducing susceptibility to angling, the main external mechanism in place to keep the walleye population in balance with the traditional forage base, i.e. yellow perch, allowing the disconnect between the 2 species to widen even further in the late 1980s. No creel survey data exist for that time period to corroborate this assertion, but adult walleye growth rates and survival were both high during years of high gizzard shad larval density (1987-1992) indicating that adult walleye were feeding well and not being removed from the system (CBFS, unpublished data). Therefore, it is possible that by the late 1980s, food web dynamics were considerably altered from the relatively stable state of walleye-perch interactions of the preceding 30 years. An amplified adult walleye population would put even greater pressure on YOY and age 1 perch than previously had been sustained, and when white perch and gizzard shad productivity crashed in the late '80s and early '90s, respectively, an already overburdened forage base of young yellow perch and walleye would have born the brunt of the pressure.

It was during this ostensibly instable period that the double-crested cormorant became established as a prominent top predator in the system, adding pressure to forage fish populations, but also presenting a new source of mortality for walleye, the top fish piscivore. These added pressures eliminated the size refuge previously realized by subadult percids, between the ages depredated through piscivory and those subjected to harvest, and contributed to some degree to declines in both yellow perch and walleye. Our estimates of consumed biomass indicate an apparently low impact through 1991, but as cormorant numbers mounted in successive years, the effect of their consumption would likely have suppressed percid populations by reducing

recruitment and directly removing adult fish, mostly yellow perch (Rudstam et al. 2004).

Admittedly, there is uncertainty in the population and diet data upon which our consumptive model and associated deductions are based. Likewise, using a flat 20% of mean body mass to estimate daily food intake oversimplifies the temporal variability in energetic requirements of breeding cormorants (Grémillet et al. 2000). However, the strength of our approach lies in the use of estimated consumption as a scalar variable, representing the changing consumptive pressures on Oneida Lake over time, and related to impact on percids in the mid- to late-1990s in previous studies by VanDeValk et al. (2002) and Rudstam et al. (2004). Furthermore, despite the apparent inconsistency of adult walleye and yellow perch populations increasing under levels of predation that approximate those hypothesized to have caused their decline initially, our standardized sampling efforts revealed that adult yellow perch and walleye populations did, in fact, increase steadily in the late 1990s and early 2000s. The resurgence of gizzard shad during this time period may have helped to buffer the impact of predation on percids, and we may not have detected the full extent of this effect in our fall diet samples. Also, while there were no changes to yellow perch harvest regulations during this period, there were restrictions imposed governing the take of adult walleye which affected survival. Our simple modeling exercise helps to elucidate the relative contributions of harvest management based on empirical changes to mortality evident from the population estimates. By altering annual survival and recruitment parameters to reflect the real and hypothetical scenarios, we gain an appreciation for the relative impacts of these variables on the adult population. The approximately 8% increase in survival, estimated to have resulted from the harvest regulations, did produce a more rapid population growth between 2001 and 2005 than did the long-term average survival. However, given the same annual recruitment,

scenarios both with and without harvest regulations imposed from 2001-2005 resulted in equivalent population sizes when projected to 2015.

In summary, cormorants on Oneida Lake have a diet consistent with a generalist feeding habit, with inter- and intra-annual variation associated with prey availability. Prey samples recovered did not simply reflect relative abundance in the system, however, and some species appeared to be continually underrepresented, indicative of some preferential or physical factor influencing their consumption. Selection by age within perch and walleye, likely associated with length and overall size, but limited by girth and gape constraints, was also evident. These selective pressures resulted in impacts to different age classes of walleye and yellow perch, with a much greater range of adult yellow perch susceptible to consumption. To add even further complexity, the impact of cormorant consumption on walleye and yellow perch populations also differed by the type of trophic interactions in which these species engage within a community context. Cormorants directly impacted walleye through predation, making cormorant-walleye interactions fairly straightforward. Given the magnitude of the annual stocking program, and the abundance of alternate forage available in Oneida Lake, it is unlikely that walleye would suffer discernibly from any indirect effects of cormorant consumption. However, a reduction in the walleye population would be beneficial to yellow perch, especially over the long-term, since depredation by walleye is the main source of mortality for the species in the first year of life (Forney 1977, Nielsen 1980). Thus, cormorants impact yellow perch through both direct and indirect interactions, which confounds our ability to construe the response of perch populations to changes in cormorant abundance, i.e. a press perturbation (Yodzis 1988, Wootton 1992, Menge 1995, Polis and Strong 1996). This is especially true when the impact of other forage species are considered, and the

effects of additional indirect interactions, like apparent competition, escalate the complexity of food web dynamics even further.

We can state, however, that the number of adult yellow perch and walleye has been increasing in Oneida Lake since the late 1990s, and that increasing recruitment of walleye, starting with the 1997 cohort, has been a driving factor for that species. It may be that the increasing numbers we have observed are the result of walleye-yellow perch dynamics being "re-set" in the mid-1990s, to a level of relative abundance that is more akin to those at which the relationship was sustained historically. It is even possible then, to consider that the negative impact of cormorant predation on the walleye population served to hasten its decline to a level that allowed yellow perch to begin to recover, which appeared to commence in the mid-1990s, a few years in advance of walleye. Given the time that has elapsed, the gaps in ancillary data such as angling effort and harvest rates, as well as the uncertainties associated with variability in annual population estimates and the strength and nature of indirect effects, the best method currently available for improving our understanding of the historic interactions between cormorant abundance and fish population dynamics in Oneida Lake is through a robust modeling exercise, preferably using the age-structured approach of Irwin et al. (2008) to first smooth out inconsistencies in the fish data. Regardless of our ability to comprehend the complexities of the biotic interactions in Oneida Lake, however, age-0 walleye and yellow perch have exhibited a declining trend in annual abundance in the last 20 years compared to previous decades, and a different suite of fish have been increasing, i.e., black basses, gizzard shad, and white perch (Hall and Rudstam 1999, Mayer et al. 2000, VanDeValk et al. 2006, Irwin et al. in press). The Oneida Lake system has experienced changing biotic and abiotic conditions in the recent past (Idrisi et al. 2001, Mayer et al. 2002, Zhu et al. 2006), and time will tell if these changes, or those on the horizon, will inevitably drive the fish community away

from the traditional walleye-yellow perch dominated system, regardless of the varying influences of cormorant predation.

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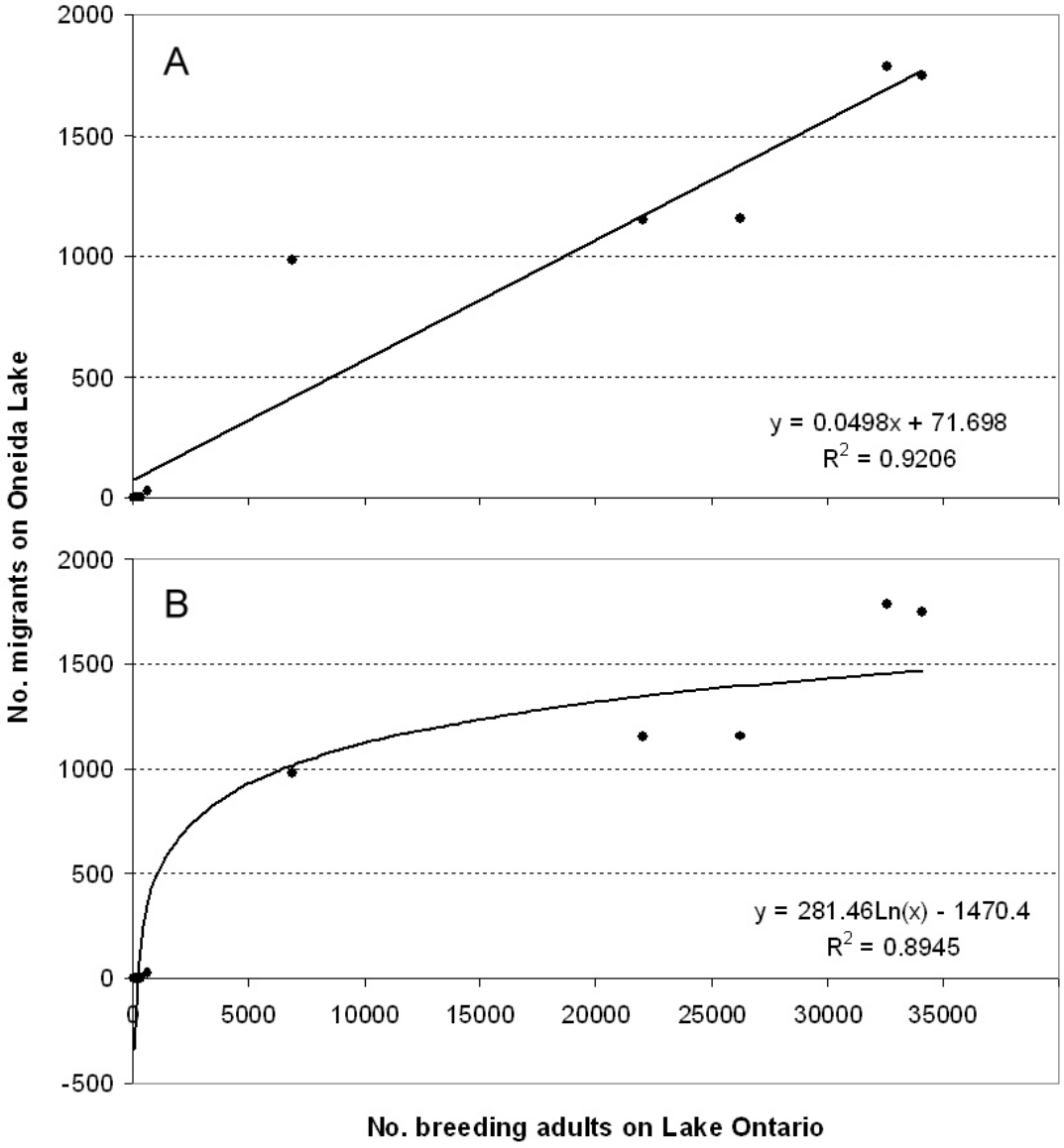
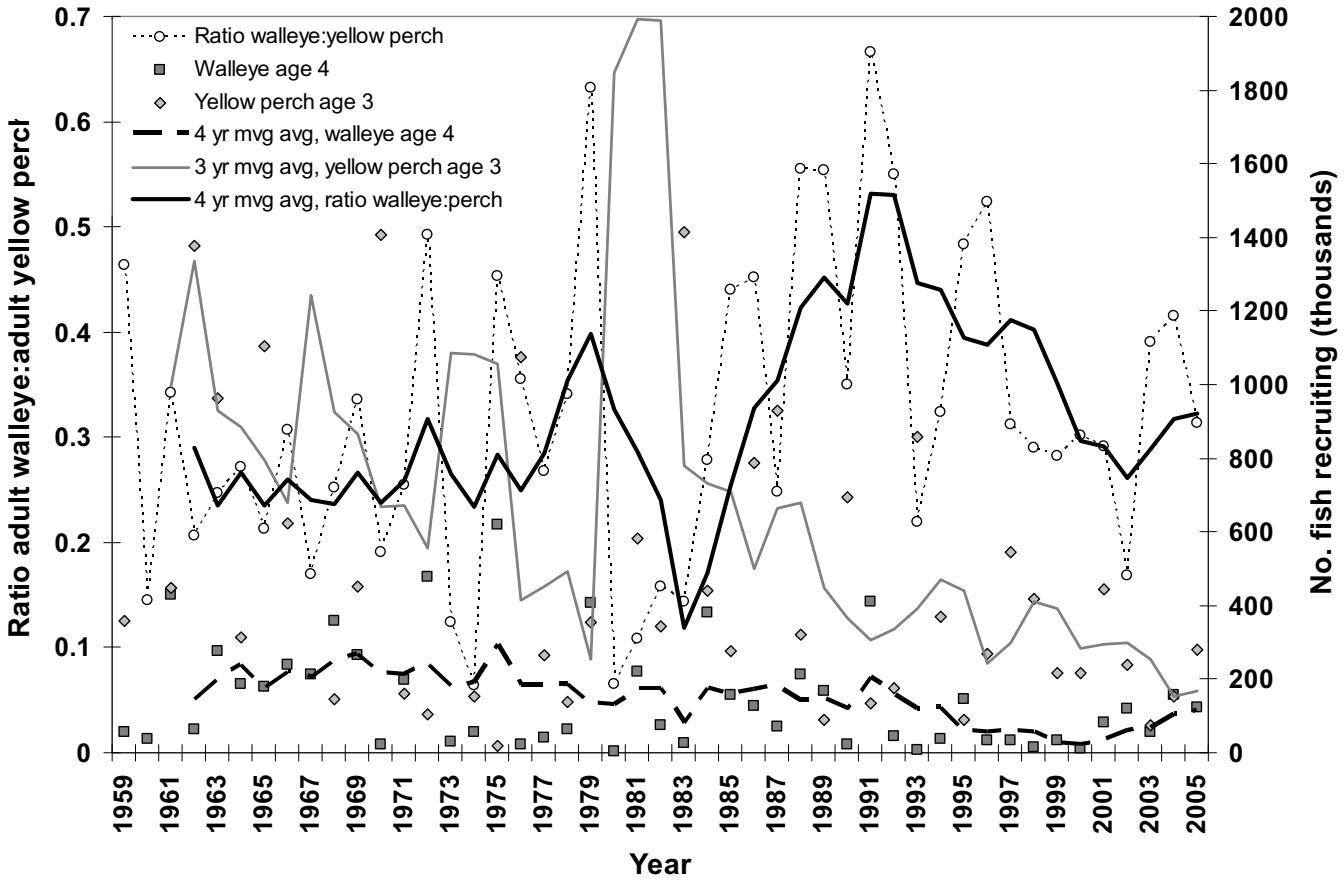
APPENDIX I

Two models used to estimate peak annual abundance of migrating double-crested cormorants stopping over at Oneida Lake from 1979-1994, derived from annual nest counts for Lake Ontario regressed on September migrant counts at Oneida Lake in 1979, ’87, ’93, ’95-’97. Model A was fit using linear regression. Model B was fit using a logarithmic expression.



APPENDIX II

The ratio of adult walleye to adult yellow perch abundance in Oneida Lake, plus the annual adult recruitment for both species (age-4 walleye, age-3 yellow perch). Moving averages, with time windows based on age of recruitment, are also depicted.



CHAPTER 4:

DAILY FORAGING PATTERNS OF ADULT DOUBLE-CRESTED CORMORANTS DURING THE BREEDING SEASON[2]

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Abstract.- We recorded the daily presence of Double-crested Cormorants (*Phalacrocorax auritus*) at the nesting island on Oneida Lake, New York, by monitoring the activities of 15 radio-tagged adults from July through September, 2000, using an automated data-logging receiver. A total of 24,464 acceptable detections was obtained for adult cormorants actively attempting to nest on the lake. Tagged cormorants were found to have a bimodal daily activity pattern during the first month, with the fewest birds detected on the island at 09:00 and 15:00 Eastern daylight time. The pattern of activity appeared to change slightly in the second month of the study,

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representative of a post-breeding period for the colony, with a shift from a less synchronous pattern of departures to a greater focus on morning activity also centered around 09:30. These results correspond with daily observations of Great Cormorant (*P. carbo*) foraging activities reported for colonies in Africa and Poland. The data also support the possibility of nocturnal foraging activity, not previously reported for this species on their summer breeding grounds. No correlation was found between total number of daily detections and climatalogical factors or events.

Key words.- Double-crested Cormorant, *Phalacrocorax auritus*, datalogger, foraging, Oneida Lake, radio transmitter

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Double-crested Cormorants (*Phalacrocorax auritus*) are colonially nesting birds whose numbers have increased rapidly throughout much of North America over the past 25 years (Weseloh and Ewins 1994; Hatch 1995; Wires *et al.* 2001). The dramatic population growth exhibited by this species has become problematic for wildlife and fisheries managers, and human interactions with cormorants now appear to have come full-circle from the conservation efforts to protect piscivorous birds in the 1970s and 1980s to a more aggressive policy of population management. Of chief concern is the ability of Double-crested Cormorants (hereafter cormorants) to impact fish populations in areas where they breed and over-winter (USDI/FWS 2003; Wires *et al.* 2001). Cormorants are opportunistic, mainly piscivorous, foragers, and have been found to exhibit spatial and temporal variation in their diet depending on location, season, and prey availability (Ludwig *et al*. 1989; Campo *et al.* 1993;

Blackwell *et al.* 1995; Blackwell and Krohn 1997; Ross and Johnson 1995; Neuman *et al.* 1997). Generally characterized as diurnal (Lewis 1929; Palmer 1962; Hatch and Weseloh 1999), cormorants are known to have night vision adequate enough to enable migration by both day and night (Mendall 1936; Palmer 1962), and have been observed foraging at night on wintering grounds (King *et al.* 1998a). Although cormorants have long been known for their foraging prowess, their reputation as insatiable fish predators is exaggerated. In a study of daily activity budgets, King *et al.* (1995) found that wintering cormorants spent an average of 17.7% of their daylight hours foraging, reflecting an active foraging effort of 7-153 min a day, with the rest of the day devoted to roosting, loafing, and flying (56.5, 18.1, and 7.7%, respectively). Foraging duration reported for breeding cormorants from the Columbia River estuary was similar, with mean daily times of 146 and 192 minutes for the months of June and July, respectively, or an average of 16% of daylight hours (Anderson *et al*. 2004). Such short foraging times are indicative of the efficiency of these predatory birds, and are common to the genus. In South Africa, for example, individuals of the congeneric species Long-tailed (Reed) Cormorant (*P. africanus*) and Great (White-breasted) Cormorant (*P. carbo lucidus*) were also found to exhibit similar efficiency, spending 26 and 19% of daylight hours foraging, respectively (Whitfield and Blaber 1979).

Early descriptions of the daily activity of breeding Double-crested Cormorants generally coincide. Cormorants are typically observed leaving their roosts around sunrise, foraging shortly thereafter, either singly or in flocks (Mackay 1894; Lewis 1929; Mendall 1936; Bartholomew 1942), then traveling to and from the nesting island intermittently throughout the day until late afternoon when they generally return to their roosts en masse in what has been described as “steady streams” of birds (Mendall 1936). These early observations correspond with more recent studies of related species, which indicate that intensity of foraging activity varies through the

course of a day (Johnsgard 1993). Based on analysis of gut contents and digestion rates, Bowmaker (1963) contended that individual Great Cormorants (*P. carbo lucidus*) in an African lake likely fed up to three times a day, with the major effort occurring in early morning and subsequent trips made to compensate for what was digested over the course of the day.

Concern over rapid growth of cormorant populations throughout the Great Lakes region of North America has spawned several studies to assess impacts to habitat and fish stocks in order to better plan the local and regional management of bird and fish populations. Spatial assessment of cormorant foraging behavior, using telemetry and aerial survey, has become critical for the quantification of impacts to these freshwater systems. Given the relatively short foraging time cormorants require to fulfill energetic needs, and the propensity for variation in foraging effort displayed by related species, it is important to know when cormorants are actively foraging so that their efforts can be accurately assessed. Studies of cormorants foraging in estuarine environments have found significant tide stage effects on diel foraging patterns (Dunn 1975; Richner 1995; Anderson *et al.* 2004), however interactions in freshwater systems are not driven by tidal events so cormorants foraging throughout the Great Lakes may exhibit different patterns. The objective of our study was to determine the times of day that radio-tagged cormorants were away from a colony site on a temperate freshwater lake in New York, and either known to be, or presumed to be, foraging. To achieve this objective, we established an automated radio receiving station on the nesting island to record the presence of tagged cormorants at fixed time intervals throughout the 24-hour day. The resulting information was used to establish foraging patterns and times to efficiently coordinate the active radio tracking of cormorant movements around the lake (see Coleman *et al.* 2005).

METHODS

Study Area

We conducted this study from 28 June to 30 September 2000, on Oneida Lake, New York. Oneida Lake has a surface area of 207 km^2 and is relatively shallow, with a maximum depth of 16.8 m and an average depth of 6.8 m. Yellow perch (*Perca flavescens*) and walleye (*Sander vitreus*) are the most abundant fish in the lake (VanDeValk *et al.* 2004), and have been estimated to constitute 58-77% of annual cormorant diet by weight on Oneida Lake since 1988 (VanDeValk *et al.* 2002; Rudstam *et al.* 2004).

Double-crested Cormorants first nested on Oneida Lake in 1984, and the colony grew from that single nesting pair to 365 pairs by 2000 (Claypoole 1988; Coleman 2003). Three small islands in the northwestern region of the lake currently provide nesting habitat for colonial waterbirds, two of which, Wantry Island and Long Island (43°14'N, 076°00'W), have been used by cormorants. Starting in 1998, cormorants nested only on Long Island, a narrow strip of mostly cobble and rock approximately 350 m long, 5-7 m wide, and no more than 0.75 m above water level during the nesting season. In 2000, all cormorant nests were either on the ground or on branches of fallen trees. High water from heavy rains in mid-May 2000 flooded the nests of roughly 2/3 of the colony, reducing the number of active nests from a peak of 365 to a post-flood peak of 206 by the first week of June. High water events such as the one experienced in May 2000 are common on Oneida and occur every few years.

Trapping and Radio Tagging

Double-crested Cormorants (N=15) were trapped on their nests between 19 and 28 June 2000, using padded leghold traps (King *et al.* 1998b). We used backpack-style radio transmitters weighing approximately 28 g (< 2% body weight), which

transmitted at a rate of 55 beats per min (ATS, Isanti, Minnesota), and attached them using a harness of 12.7 mm (0.5 in.) Teflon ribbon (Dunstan 1972; King *et al.* 2000). All cormorants were banded with USFWS aluminum bands and were fitted with yellow patagial tags to allow individual recognition.

The cormorants selected for this study were trapped on nests rebuilt after high waters receded. Trapping was delayed until late June to allow sufficient time for adults to invest in the renesting effort. While none of the adults in our study are known to have fledged chicks, all tended their nests for several days after capture, and hatching occurred in 5 of the 15 nests of radio-tagged birds. The failure rate of the tagged birds was not unusual when compared to the lower nest success of other cormorants in this late cohort of renesters. Most failures were due to intense gull predation, potentially exacerbated by human disturbance. Researcher presence may also have contributed to lower success, but data collection methods were no different in 2000 than those employed in more successful years.

Data Logging System

We established an automated receiving station on Long Island to detect radio transmitters at the colony site. Due to the potential for access of the island by the general public, and the exposure of the site to the elements, a lockable box was constructed to protect the electronic equipment. We installed a 1.44 m^2 concrete slab on Long Island near the center of the nesting area and bolted two lockable boxes to the slab: a large outer box, with interior dimensions of 91 x 79 x 61 cm, and an inner Army-surplus ammunition box to house the receiving and logging components of the station. An antenna mast, made of 38 mm (1.5 in.) galvanized pipe, was embedded in the concrete along with a 2.4 m grounding rod. The station was powered by a 12 volt marine battery, maintained by a photovoltaic panel mounted to the outside of the outer box (Solarex model MSX-10L, Frederick, Maryland). An omnidirectional dipole

antenna (Cushcraft Corp. model CRS-150, Manchester, New Hampshire) was mounted to the mast, achieving a height of approximately 2.5 m from the surface of the island.

We used an ATS model R2100 receiver and a model D5041 data collection computer to record presence/absence information for each radio transmitter over pre-set time intervals. The receiver was programmed to record the date and time of transmissions detected within a small range of rates, roughly 53 - 57 beats per min, to filter out extraneous signals from radio interference or diving activity (see below). Detections were only accepted if they fell within the expected range, so partial or discordant signals were not recorded. A dummy transmitter was positioned on Long Island to verify daily logger function. We downloaded the data to a laptop computer during weekly trips to the island to collect regurgitated materials for diet analysis. Such visits were brief, lasting approximately 15 min, and occurred at varying times during daylight hours. Cormorants displaced by these activities remained close to the island, and would quickly return after our departure.

The sensitivity and sampling rate of the receiver were adjusted three times over the season in response to changes in cormorant behavior and management practices. While the probability of accurately detecting tagged cormorants varied between periods, we assumed detectability to be constant within each of the time periods. Initially, the receiver was tuned to cover only the nesting area, where nearly all birds resided. This was accomplished by adjusting the gain of the receiver to detect transmitters positioned approximately 50 m distant, but not further, thereby encompassing all the cormorant nests on the island. During this time period (Period 1; 29 June - 1 August), the receiver/logger scanned each transmitter frequency once every 15 min for 15 sec duration. Chicks and eggs were still being tended regularly

during this time, and the high rate of sampling was intended to produce precise estimates of cormorant presence at the nesting area.

During the second period of the study (Period 2; 3 August - 2 September) cormorants at the colony had either fledged chicks or had abandoned their nesting effort, and no longer roosted or loafed in the nesting area. Given the reduced nesting activity, we increased the sensitivity (gain) of the receiver so that transmitters carried to the farthest ends of the island were still detectable (approx. 200 m). We also reset the receiver to scan each frequency once every 30 min for 30 sec intervals. The increase to a 30 sec scan interval was intended to help distinguish between birds loafing or roosting on the island versus those foraging in nearby waters now within range of detection. Once submerged, our transmitters were not detectable, so the 30 sec duration was designed to exceed the 15 - 20 sec surface intervals commonly observed between the dives of foraging cormorants.

A cormorant management program, implemented annually from 1998 to 2003, was commenced on 5 September in 2000. The goal of the program was to remove all resident and migratory Double-crested Cormorants from Oneida Lake through "hazing" – the active and passive disruption of roosting, loafing, and foraging cormorants (Chipman *et al.* 1998, 2000). To track the impact of the hazing program on the behavior of resident cormorants, we increased the sensitivity (range) of the receiver again on 3 September to reach nearby Wantry Island (>1500 m), but the sampling rate and scan interval remained the same as in Period 2. These settings were maintained throughout the remainder of the study (Period 3) until we disassembled the logger on 30 September.

Data Analysis

We examined the number of detections by half-hour block for all cormorants in Periods 1 and 2 to explore general 24-hour presence patterns for tagged birds on

Long Island prior to management. To control for bias due to variation in the number of detections by bird (i.e. unequal representation of individual birds in the aggregated data), count data were normalized through the calculation of Z-scores by half-hour intervals for each individual using the formula: $Z_i = (x_i - \bar{x})/s$, where $\bar{x}$ is the sample mean and s is the sample standard deviation (Abdi 2007). We then determined mean Z-score values for all birds by half-hour. Normalizing the data also controlled for changes to the sampling parameters, and allowed for a direct comparison of detections between Periods 1 and 2. Cumulative numbers of detections were also computed for each day, as well as for individual birds, for all 3 time-periods. Daily detection totals were analyzed for influence of weather conditions and meteorological effects based on archived climatological data recorded at Hancock International Airport in Syracuse, New York, located approximately 15 km from the receiving station (National Weather Service, National Oceanic and Atmospheric Administration). The following variables were tested for possible correlations with the number of radio detections per day: average temperature, average wind speed, total precipitation, and the proportion of daily sunshine received. These variables were selected to examine the impact of storm events, and associated wave action and water clarity effects, on daily foraging effort. Daily sun exposure data, a measure of cloud-cover, and moon phase information were also used to estimate ambient light conditions at night for Periods 1 and 2. These data were compared to nightly detection totals (19:00 - 05:30) to test for possible correlation between ambient light and nocturnal foraging.

RESULTS

The datalogger recorded 24,464 acceptable detections (or "hits") for all 15 radio-tagged cormorants from 28 June - 30 September 2000 (Periods 1, 2, and 3). Frequency of detection varied among individuals (Fig. 4.1), and ranged from 166 to

1923 (mean = 699) in Period 1 and 494 to 1171 (mean = 873) in Period 2. All 15 radios remained active through the three time periods, however not every cormorant remained on Oneida Lake for the duration of the study (e.g., one cormorant left the lake on 29 July and was detected only 11 times in Period 2). The probability of detection and/or acceptance of detected signals increased from Period 1 to Period 2 due to adjustment of the receiver's sensitivity. The change in transmitter detectability resulted in a higher proportion of hits (presence) to misses (absence) recorded in Period 2 (Fig. 4.2), and an increase in the number of individual cormorants recorded at each hourly interval during the day (Fig. 4.3).

During the 33 days from 29 June - 1 August (Period 1), transmitters were detected at the colony 10,480 times. Plots of both the total number of detections and mean Z-scores for individual birds by half-hour reveal a bimodal pattern with the fewest detections around 09:00 and again at 15:30 (all times are Eastern daylight time: GMT – 4h) (Fig. 4.4). The number of hits per half-hour during these two peak foraging times averaged only 117 (mean Z-score = -1.12), less than half the number of detections from 19:00-05:30 (mean no hits/half-hour = 295, mean Z-score = 0.80). The data also indicate that cormorants generally began leaving Long Island after 05:30, which corresponds with sunrise during this period (05:28-05:56 from 29 June - 1 August). Tagged cormorants were generally detected with increasing frequency starting at 16:00, and by 18:30, more than two hours before sunset (20:48-20:25), the majority of tagged birds (relative to the number detected that same night) were usually back at the colony site (Fig. 4.3).

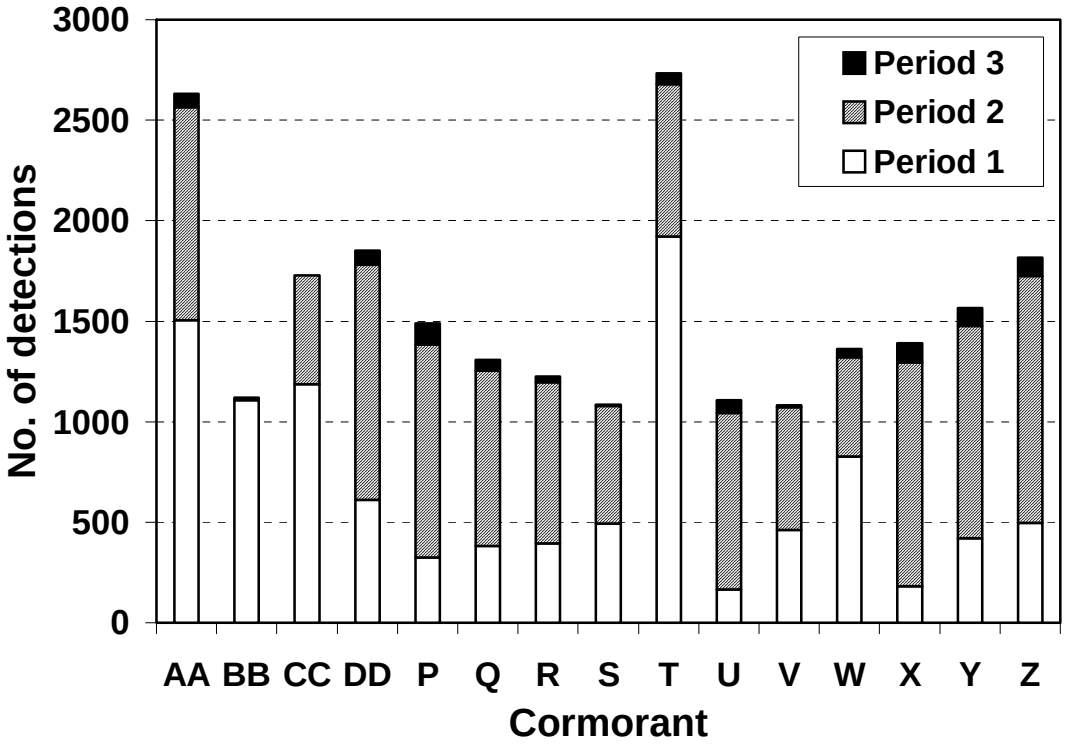
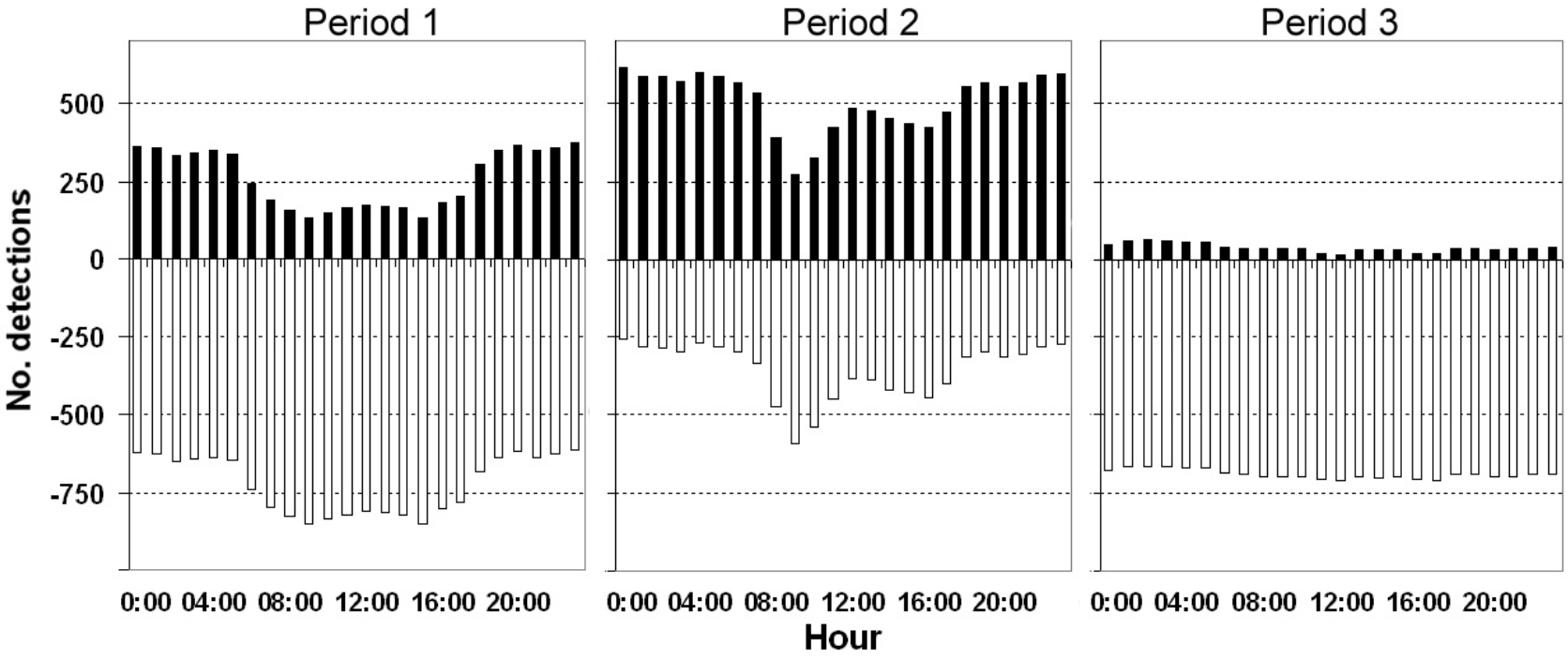


Figure 4.1. Cumulative number of detections by individual bird for 15 radio-tagged cormorants on Oneida Lake, New York, in 2000. Time Period 1 represents 29 June - 1 August, Period 2 represents 3 August - 2 September, and Period 3 represents 4 September - 30 September. Bird BB left the lake on 29 July, and was detected only sporadically on Oneida Lake after that date.

Figure 4.2. Presence/absence data by hour for 15 Double-crested Cormorants at the colony roosting site on Oneida Lake, New York, for 3 time periods in 2000 (Period 1: 29 June - 1 August; Period 2: 3 August - 2 September; Period 3: 4 September - 30 September). Black bars (positive values) represent total transmitter detections by hour through the entire time period; white bars (negative values) represent failed detections based on the maximum number theoretically possible given a 30 min sampling rate for all three time periods (Period 1 data sub-sampled by 30 min). The time of day is presented in Eastern daylight saving time (GMT – 4 hours). The range of reception was set to detect the 15 tagged birds at their core nesting and roosting area. As the season progressed, we expanded the range to detect birds that left the core area but continued to use other parts of the island. Detection range was smallest in Period 1, ~50 m, increased to ~200 m in Period 2, and was maximized in Period 3 to ~1500+ m


Period 1
Period 2
Period 3
500
250
0
-250
-500
-750
No. detections
0:00 04:00 08:00 12:00 16:00 20:00
0:00 04:00 08:00 12:00 16:00 20:00
0:00 04:00 08:00 12:00 16:00 20:00
Hour

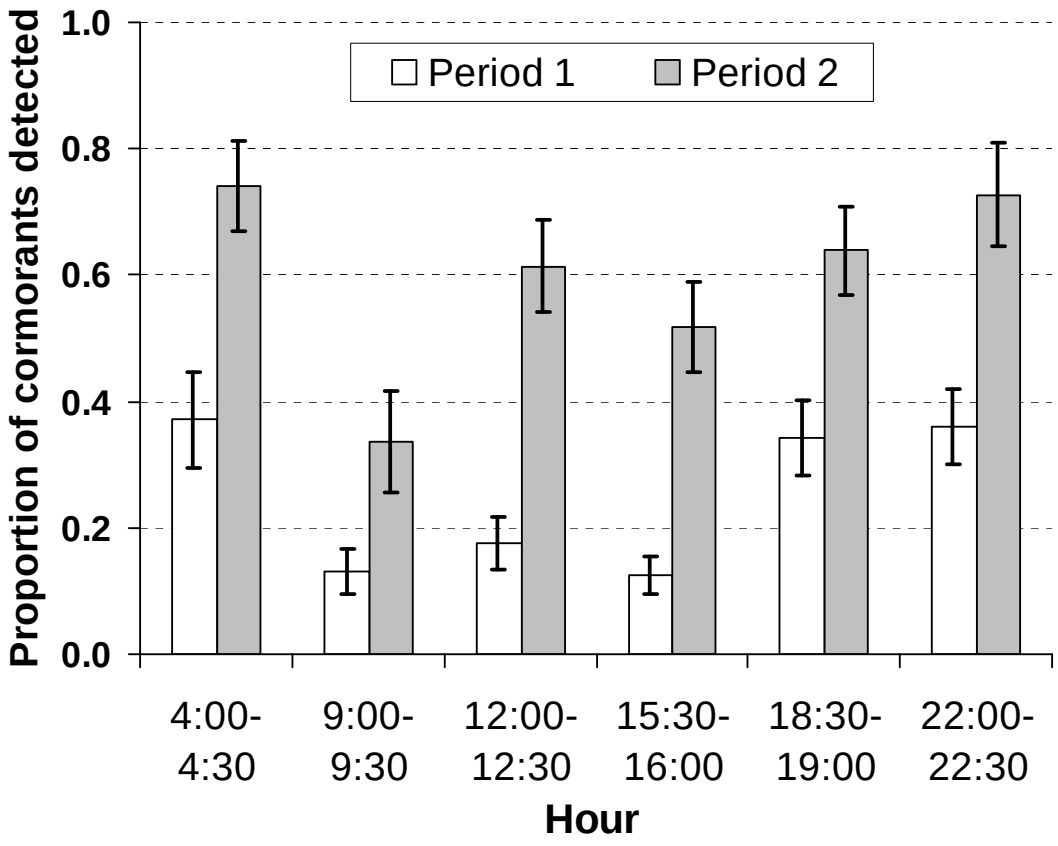


Figure 4.3. Proportion of radio-tagged cormorants detected at the colony on Oneida Lake, New York, by half-hour block for 6 key times of day: pre-dawn, peak morning activity, mid-day, peak afternoon activity, approx. 1-2 hrs before sunset, and nighttime. Columns represent mean values for all days in time Period 1 (29 June - 1 August, 2000) and Period 2 (3 August - 2 September, 2000). Error bars are ± 2 SE.

From 3 August - 2 September (Period 2), the datalogger, scanning once every 30 min, recorded 12,238 hits. These data represent regular detections of 14 cormorants, excluding the bird that left Oneida Lake on 29 July and was later found on a nearby lake. Because the reception range was slightly expanded, detected birds in Period 2 could have been loafing anywhere on Long Island or sitting on the water near by. Although a plot of detections and mean Z-scores for hits by half-hour in Period 2 reveals a pattern similar to Period 1, the absence of detections in the morning, maximized at 09:30, is more conspicuous than the absence in the afternoon (Fig. 4.5). The decline in the number of hits through early morning is also more rapid than during Period 1, indicating a more synchronous departure during the second time period. The average number of detections during peak morning activity (09:00-10:00) was 138 per half-hour (mean Z-score = -1.99), again just less than half the number of hits recorded over nighttime hours (mean no hits/half-hour = 291, mean Z-score = 0.55). The afternoon mode, clearly evident during July (Period 1), was greatly diminished in Period 2, however, with a mean of 220 hits/half-hour and an average Z-score of –0.44. The data in Period 2 also indicate a later departure time from the island, which coincides with a later sunrise over these 31 days (from 05:56-06:29). By 18:00 a large proportion of tagged cormorants were detected back at the island, again well before sunset (19:36-20:24) (Fig. 4.3).

Period 3, which began on 4 September, preceded by 1 day the cormorant hazing program, which effectively scattered the birds and disrupted the use of Long Island as a roosting and loafing area. As a result, analysis of cormorant activity on a 24-hour scale, as detailed above, was not possible. To improve our chances of detecting scattered birds, we increased the sensitivity of the receiver in Period 3, expanding the reception range to include several nearby islands and loafing sites. Aside from infrequent daily visits, all but three tagged cormorants left Oneida Lake

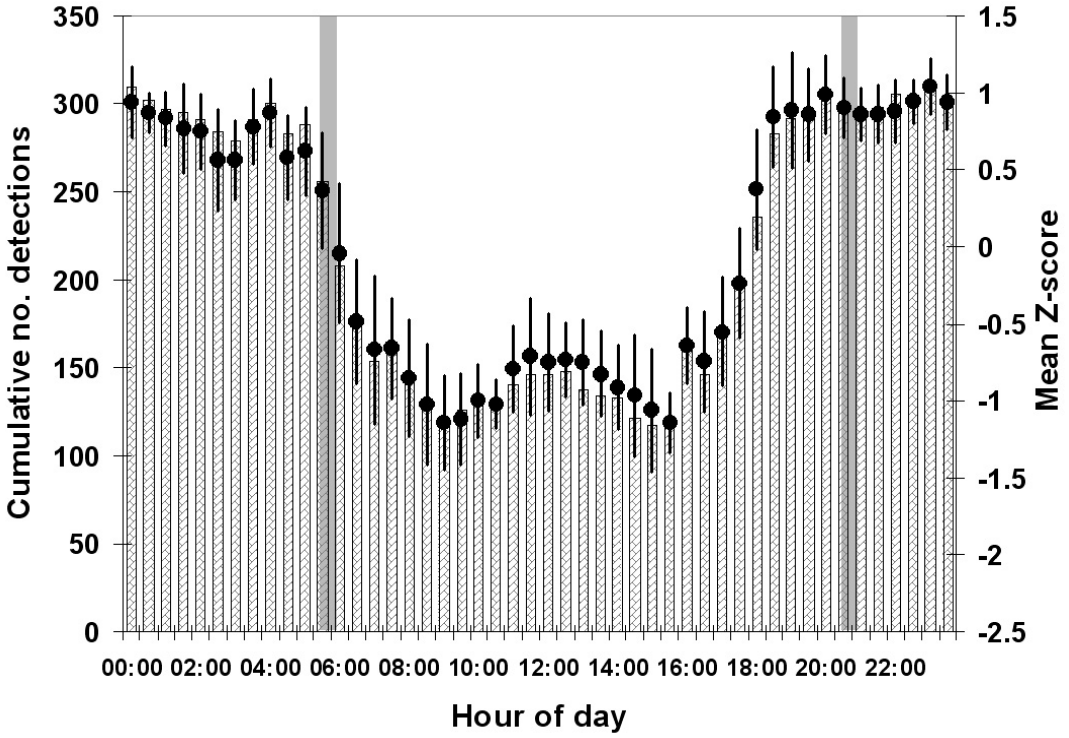


Figure 4.4. Cormorant activity for Period 1 (29 June – 1 August, 2000). Total number of transmitter detections (columns) and mean Z-scores (points) for individual cormorants by half-hour at the colony site on Oneida Lake, New York. Detections are for 15 Double-crested Cormorants trapped on nests on Oneida Lake between 19 and 28 June, 2000. Z-score error bars are ± 2 SE. Width of solid gray bars indicates the range of sunrise (05:28 h-05:56 h) and sunset (20:48 h-20:25 h) for Period 1. The time of day is presented in Eastern daylight saving time (GMT – 4 hours). The range of detection during Period 1 was centered around the nesting region of Long Island (approx. 50 m).

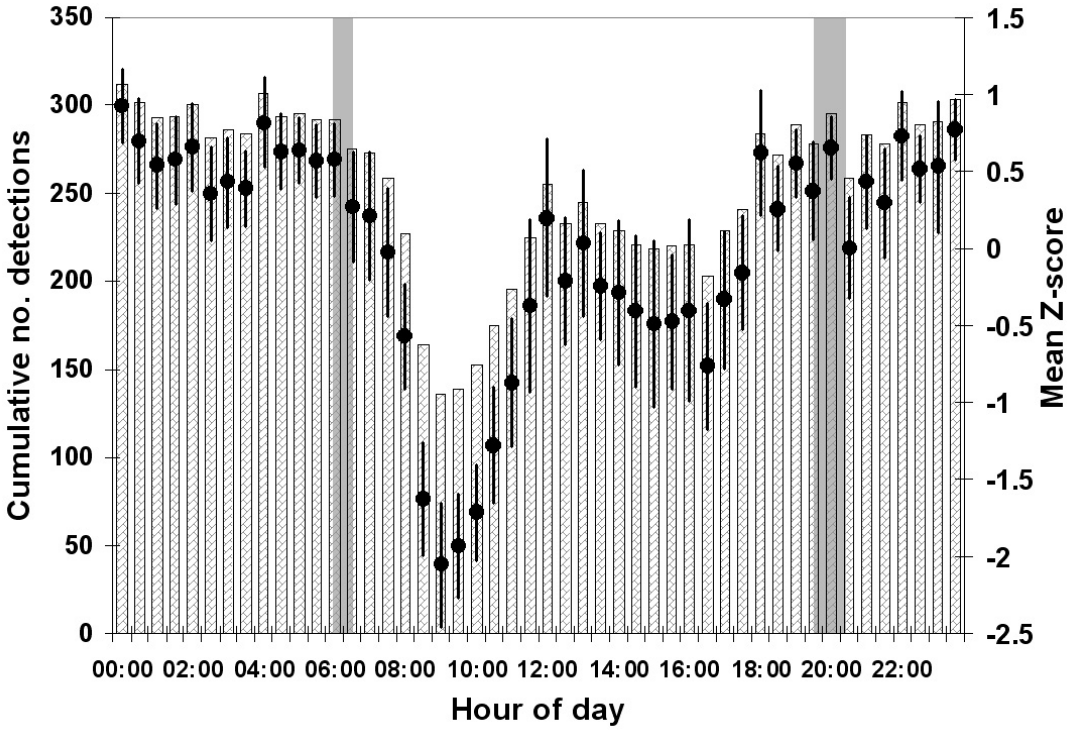
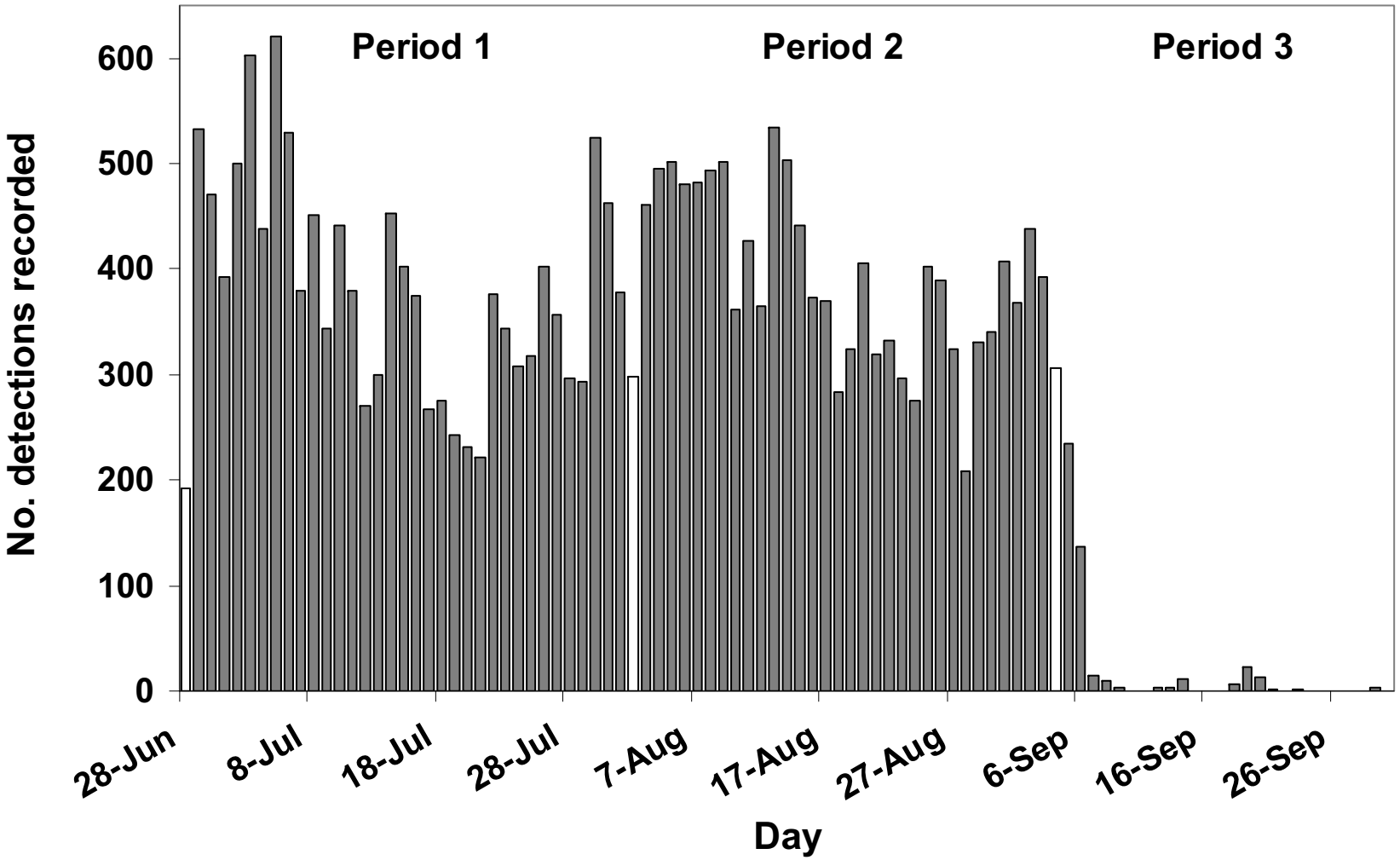


Figure 4.5. Cormorant activity for Period 2 (3 August – 2 September, 2000). Total number of transmitter detections (columns) and mean Z-scores (points) for individual cormorants by half-hour at the colony site on Oneida Lake, New York. Detections are for 14 Double-crested Cormorants trapped on nests on Oneida Lake between 19 and 28 June, 2000 (one bird left the lake on 29 July). Z-score error bars are ± 2 SE. Width of solid gray bars indicates the range of sunrise (05:58 h-06:30 h) and sunset (20:23 h-19:37 h) for Period 2. Time of day is presented in Eastern daylight saving time (GMT – 4 hours). The range of detection during Period 2 was all of Long Island and surrounding waters (approx. 200 m).

Figure 4.6. Cumulative number of detections by day for 15 radio-tagged cormorants on Oneida Lake, New York, in 2000. White bars delineate breaks between time Period 1 (29 June - 1 August), Period 2 (3 August - 2 September), and Period 3 (4 September - 30 September). The cormorant hazing program was initiated on 5 September, thus accounting for the rapid decline.


Period 1
Period 2
Period 3
No. detections recorded
600
500
400
300
200
100
0
28-Jun
8-Jul
18-Jul
28-Jul
7-Aug
17-Aug
27-Aug
6-Sep
16-Sep
26-Sep
Day

immediately after the hazing program was initiated, as was the case for most cormorants on the lake. The observed movement of cormorants off of Oneida Lake was documented by the distinct lack of detections recorded by the datalogger, and further supported by declining daily counts around the lake (unpublished data). The dramatic decline in the number of daily cormorant detections on and around Long Island followed precisely the initiation of cormorant management on 5 September (Fig. 4.6), and numbers remained low throughout the month.

No significant correlations were found between the cumulative number of detections per day and the climatological factors tested in Periods 1 and 2. Correlation with average daily temperature approached significance in Period 2 (r_{31} = 0.33, P = 0.06), but was not significant in Period 1 (r_{32} = 0.12, P = 0.52). Furthermore, despite the fact that several birds appeared to have left Long Island temporarily on many different nights, evident as reduced presence from 2:30 to 3:30 (Figs. 4.4 & 4.5), there was no correlation between cumulative nightly detections and daily cloud-cover in either period (r_{32} = -0.09, P = 0.60, and r_{33} = 0.18, P = 0.31 in Periods 1 and 2, respectively), nor any evident trends associated with moon phase.

DISCUSSION

Our results confirm descriptions from early observational investigations of Double-crested Cormorants (Mackay 1894; Lewis 1929; Mendall 1936; Bartholomew 1942), and support a bimodal pattern of daily foraging effort focused around 09:00 and 15:30 (Figs. 4.4 & 4.5). This pattern was most evident on Oneida Lake during mid-nesting season (Period 1; 29 June – 1 August), when most tagged birds were tending nests and the colony's successful cormorants were rearing chicks. These results are similar to those of Bowmaker (1963), who proposed that foraging efforts of Great Cormorants in Africa were highest from dawn to around 10:00 hrs, falling to

virtually no effort from 12:00 to 14:00 hrs, then renewing in intensity from 14:00 to 18:00 hrs. Another similar pattern has also been described for Great Cormorants (*P. carbo sinensis*) breeding near the Baltic Sea in Poland (Goc *et al*. 1997, 2003). Those studies, which ran from March to August, also revealed a mostly bimodal pattern in the number of birds leaving the colony in May and June, with most cormorants leaving around dawn, and again during mid-afternoon (approx. 15:00 Central European time). Interestingly, Goc *et al*. (2003) also observed a shift from a more bimodal departure pattern in their mid-season, akin to Period 1, to a more asymmetric pattern later in the season, characterized by a peak morning effort between 07:00 and 09:00. The remarkably similar pattern observed by Goc *et al.* (1997, 2003) to that of this study (Fig. 4.5) suggests that the general shift in cormorant foraging behavior we observed during the breeding season may not be linked to increasing availability of prey in the form of growing age-0 fish, as we originally hypothesized, but rather to the breeding condition of nesting birds. Adults tending nests may have a more balanced daily foraging pattern, presumably driven by higher energetic requirements of egg production and temporal demands on both adults for nest attendance and incubation. Once free from nesting obligations, either through successfully fledging chicks or, in the case of this study, nest abandonment, cormorant foraging behavior shifts to reflect the importance of a significant morning effort followed by sporadic trips during the remainder of the day to replenish digested stomach contents, as suggested by Bowmaker (1963). The degree to which afternoon foraging is less synchronous and more individualistic is represented by the greater variability in afternoon presence on the nesting island compared to morning values (see error bars in Fig. 4.5). Analysis of the spatial distribution of foraging locations for cormorants on Oneida Lake also revealed that distances to those locations were significantly greater during morning hours than in the afternoon (Coleman *et al.* 2005), further evidence of the

disproportionate daily foraging efforts captured by the data logger in the post-breeding period (Period 2). Given the similarity between the activity pattern described in this study and those observed in Africa and Europe (Bowmaker 1963; Whitfield and Blaber 1979; Richner 1995; Goc *et al.* 1997, 2003), it is likely that this general pattern, as depicted in Figure 4.5, is a standard post- or non-breeding approach to foraging utilized by different species of cormorant when prey are uniformly available. Diel variation in prey availability, such as those resulting from tidal stage or spawning migration, are special conditions under which these flexible predators will alter this pattern in order to capitalize.

Weather conditions and events were not found to influence the daily number of detections for cormorants on the nesting island, nor was a correlation revealed between absence at night and cloud cover/visibility. However, evidence of nocturnal foraging activity was indicated by the data, which revealed variable numbers of hits for nighttime hours. The decline in the number of detections between 00:00 and 04:00 in both time periods, for example, implies that some birds left Long Island during early morning hours, but returned by 04:00 (Figs. 4.4 & 4.5). Such departures from the nesting island are apparent through inspection of individual records on a daily time scale. Individual cormorants regularly detected on the island in the evening and early at night would, occasionally, fail to be detected over several scan intervals during the night, but would reappear in the early morning before sunrise. We chose not to depict these data because cormorants are known to migrate at night (Palmer 1962), and the actual behavior and location of the missing birds cannot be accurately determined from these presence/absence data. However, based on the brief duration of their absences, birds that left the island at night, then reappeared before sunrise, had likely been foraging. The presence of other birds during these times supports the absence of a general disturbance that might have moved birds out of the colony. Also, the

relatively short duration of absences is not suggestive of long distance movements during that time. Double-crested Cormorants have previously been observed foraging on a moonless night in their Mississippi wintering grounds (King *et al.* 1998a), and Great Cormorants have been found capable of successfully foraging in the low light conditions of Arctic winter in Greenland (Grémillet *et al*. 2005), so our assertions here are certainly feasible. Further, the lack of a significant correlation between daily weather conditions and time cormorants spent on the nesting island should not be interpreted as a failure of weather to impact foraging activity. As visual predators, cormorant foraging efficiency is vulnerable to the effects of turbidity (Bell-Cross 1974; Abrahams and Kattenfeld 1997; Strod *et al*. 2004), and we hypothesized that the effects of wind, rain, and cloud cover on water clarity and lake conditions would result in a perceptible difference in foraging effort, similar to what Grémillet *et al*. (2005) found for Great Cormorants foraging under low light conditions. Greater resolution in weather data would be required to pursue this more conclusively.

Evidence of pre-migratory long distance movements was also revealed by the datalogger. As part of a collaborative effort to track cormorant movements between colonies on a larger scale, radio frequencies of cormorants tagged by biologists with the New York State Department of Environmental Conservation on Little Galloo Island, in eastern Lake Ontario, were also programmed into the receiver in Periods 2 and 3 (Mazzocchi 2001). Oneida Lake serves as a staging area for migrating cormorants in late summer, and until the autumn management plan was initiated in 1998, the number of birds would swell from a resident population of approximately 700 to over 2000 individuals by mid September (C. Adams, New York State Department of Environmental Conservation, pers. comm.). The origin of these migrants was unknown, but thought to be the colonies in eastern Lake Ontario. Proof of this connection was lacking until cormorants radio-tagged on Little Galloo Island,

which supported the largest cormorant colony in Lake Ontario until 1999 (Weseloh *et al*. 2002), were detected by the automated receiver on Oneida Lake. Many of these individuals were first recorded during nighttime hours, between 23:00 and 04:00, further evidence of the nocturnal activities of this species. It is unknown if the birds made the 80 km flight from the Little Galloo colony directly to Long Island at those hours, or if they had been roosting locally and only arrived on Long Island at those times.

The results presented here confirm previous observations of daily cormorant activity; however, they also raise additional questions about foraging behavior. The potential for differences in behavior attributable to sex, unfortunately outside the scope of this study (see Coleman *et al*. 2005), may explain some of the observed variation in detectability. The changes in activity patterns we found between the hatching/chick-rearing period and the pre-migration period, and the correspondence with similar foraging patterns at many colonies of congeners, warrants further study to explore the links with seasonal changes in prey availability and the energy requirements of adult cormorants at different stages of the breeding cycle. The fact that none of the cormorants followed in this study succeeded in fledging a chick prevents us from drawing inference about the behavior of successful adults during the chick rearing period. However, breeding adults not delayed by early season weather events, or other setbacks, are often independent of their fledged chicks by August on Oneida Lake, and may then behave in a manner similar to adults that failed to rear chicks. One could postulate that the same patterns might also be exhibited by immature non-breeders and juveniles engaged in social foraging with adults. Likewise, we are also aware that the cormorants in this study were exposed to some level of disturbance from initial capture, weekly data collection, and radio-tagging. We are unable to measure any of these effects on daily foraging behavior in this study;

however, given that all the birds survived the 2+ months of the study, and that the majority remained on Oneida Lake until they were forced off by hazing, we are confident that these birds experienced conditions that were not outside their comfort range. Furthermore, as large-scale cormorant nest management programs spread through Great Lakes states and provinces (NYSDEC 2004; MDNR 2005; USDA/APHIS 2004, 2005; OMNR 2006), we assert that the conditions under which we conducted this study will be increasingly relevant to those experienced by Double-crested Cormorants throughout the region.

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CHAPTER 5:

DIVING BEHAVIOR AND FORAGING EFFORT OF THE DOUBLE-CRESTED CORMORANT (PHALACROCORAX AURITUS) AT THREE NEW YORK COLONIES[3]

Abstract: In 2002 we initiated a 2-year study of double-crested cormorant foraging behavior to complement ongoing impact analyses and to compare cormorant foraging effort on Oneida Lake, New York, with other lakes of differing morphometry and prey composition. We deployed electronic time-depth recorders (TDRs) on adult cormorants from colonies on Oneida Lake, Lake Ontario, and Lake Champlain to record the time, duration, and depth profiles of foraging dives over several days during the breeding season. Discounting the first day(s) as an acclimation period, and any partial last days, 491 full days of activity were recovered for 22 individuals, during which the TDRs recorded 88,000 dives. Duration of individual deployment ranged from 3 to 55 days, and repeated measures ANOVA revealed no significant difference between lakes in the daily number of dives performed by individual, or the total amount of time spent underwater each day. Because we selected larger birds, 17 of the 22 cormorants were male, and all 5 females were captured on Oneida Lake. Maximum dive depths varied by individual and by lake, and differences in dive depth by lake was borderline significant. Cormorants foraged at deeper depths on Lake Ontario and Oneida Lake, and the maximum depth we recovered (25.8 m) was recorded at Lake Ontario. The maximum depth recorded on Lake Champlain, however, was just 8.6 m. No difference in dive depth or total daily dive time was

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detected by sex or physical size (body mass and wing chord). Julian day did significantly affect maximum diving depths, which exhibited a trend towards deeper dives through the season on both Lake Ontario and Lake Champlain. Mean individual dive durations ranged from 17 – 34 sec, and the overall mean duration was 22 ± 10 sec ($\overline{x}$ ± 1 SD). Mean values by lake for the total amount of time cormorants spent diving (underwater) ranged from 62 – 70 min, and the overall mean for all birds was 66 ± 37 min ($\overline{x}$ ± 1 SD). Timing of diving activity was most similar between Oneida Lake and Lake Champlain, with a bimodal activity pattern focusing on late morning and late afternoon foraging activity. Very little dive activity was recorded before dawn or after dusk on Oneida Lake and Lake Champlain. The activity pattern for Lake Ontario differed from those of the other lakes, with the initiation of foraging activity occurring in the twilight pre-dawn period, and the lack of a defined peak activity time in the morning. The results from the three systems reveal a great degree of flexibility in foraging strategy and diving behavior, likely associated with prey distribution and availability.

Key words: cormorant, dive profile, foraging, Great Lakes, Oneida Lake, *Phalacrocorax auritus*, predator-prey, release device, spatial interaction, TDR, time-depth recorder

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Cormorants and shags, of the family Phalacrocoracidae, are capable of diving to great depths in search of aquatic prey. With approximately 37 extant species currently recognized (Siegel-Causey 1988, Johnsgard 1993), and a virtually worldwide distribution, cormorants are found across many different ecozones and aquatic environments. While not all species have been extensively studied, the diving

behavior of many in the family has been investigated, revealing considerable diversity in habit and capability. Of the species that have been studied, many were found to dive routinely to 20-60 m (Croxall et al. 1991; Watanuki 1996, 2008; Wanless 1997; Grémillet 1999), and one species, the Crozet shag (*Phalacrocorax melanogenis*) was observed to reach 145 m (Tremblay et al. 2005), an incredible depth for a flighted bird to dive. Cormorants and shags are foot-propelled divers that generally forage in the benthic and demersal zones, but they also feed readily on pelagic species in the open water (Craven and Lev 1987; Ludwig et al. 1989; Wanless et al. 1991, 1999; Campo et al. 1993; Blackwell et al. 1995, 1997; Ross and Johnson 1995; Watanuki et al. 1996, 2004; Neuman et al. 1997; Grémillet et al. 1999; Kato et al. 2001; Coleman et al. *in review*, 2009, Chapter 3). Energy requirements differ by species and by season, but cormorants have generally been found to consume approximately 20% of their body weight daily (Dunn 1975, Glahn and Brugger 1995, Grémillet et al. 2000, Engström 2001), and their flexibility and physiological abilities enable them to be very effective fish predators. Daily foraging efforts are influenced by multiple environmental factors, however, including prey type and density, water depth, turbidity, and seasonal or climatic effects such as temperature (Croxall et al. 1991; Monaghan et al. 1994; Abrahams and Kattenfeld 1997; Kato et al. 2001; Grémillet et al. 2003; Strod et al. 2004; Enstipp et al. 2006, 2007). Thus it is possible for birds in the same geographical region to experience very different foraging imperatives depending on the locations they choose to inhabit.

Despite its widespread distribution in North America, rapid population growth, and the associated concerns regarding impacts to fish populations, the double-crested cormorant (*P. auritus*) is a species that has avoided the academic scrutiny to which the foraging behavior of congeners has been exposed. There is little current information available about the diving abilities and habits of wild double-crested cormorants,

however, the underwater performance and physiology of this species have been the target of recent studies with captive animals (see Enstipp et al. 2001, 2006, 2007; Grémillet et al. 2006). Observational studies of double-crested cormorants have provided some insight into their diving abilities, foraging strategies, and habitat use (Munro 1927, Lewis 1929, Mendall 1936, Bartholomew 1942, Custer and Bunck 1992, Stapanian et al. 2002, Anderson et al. 2004, Coleman et al. 2005, Duerr 2007), but there is little information in the published literature detailing daily dive characteristics and depth utilization, both of which relate directly to energetic requirements and bird-fish spatial interactions. In addition to the value of such data for our basic knowledge of the species and its role in aquatic systems, they are important to the advancement of our understanding of the consumptive impacts of double-crested cormorants on freshwater systems in North America, and the associated debate regarding the potential for negative impacts that continues to wage among anglers, aquaculturists, special interest groups, and resource managers, on all sides of this issue (Glahn and Brugger 1995; Wires et al. 2001, 2003; USDI/FWS 2003; Diana et al. 2006).

The purpose of our study was to characterize, the diving abilities and underwater foraging habits of double-crested cormorants, hereafter cormorants, at their breeding grounds in the northeastern U.S., and to compare foraging effort in 3 lakes (Lake Ontario, Oneida Lake, and Lake Champlain) with disparate bathymetric profiles. The cormorant colonies in eastern Lake Ontario, Oneida Lake, and Lake Champlain were, and were also sites where concurrent and recent research efforts could provide additional information on fish assemblages, cormorant diet, and local movements (Weseloh et al. 2002; Ross and Johnson 1995; Ross et al. 2004; Duerr 2007; Coleman 2009, Chapter 2). We deployed electronic time-depth recorders (TDRs) on free ranging adult cormorants at these three sites to monitor diving activity

over several days during the breeding period. The objectives of this study were: 1) to examine the daily dive pattern of cormorants at each of the three sites, 2) to characterize the amount of time that cormorants spent diving each day and compare foraging effort, defined here as time spent diving, between the three lakes, 3) to investigate the diving capability of the species and examine depth utilization at each location, and 4) to test if maximum dive depths or daily foraging effort were affected by physical attributes of individual birds (sex, body size) or by attributes associated with diel or seasonal chronology.

METHODS

Study area

We deployed TDRs on cormorants at three different colonies in New York State. In 2002, we fitted 10 cormorants with TDRs on Little Galloo Island in eastern Lake Ontario (28 May; 43°53'N, 076°23'W), and 13 cormorants at the colony on Long Island in Oneida Lake (29 June; 43°14'N, 076°00'W). In 2003, we deployed TDRs on 10 cormorants at the Four Brothers Islands in Lake Champlain (3 July; 44°25'N, 073°20'W), and another 31 cormorants on Oneida Lake (9 June – 23 July). Deployments at Lake Ontario and Lake Champlain were accomplished through collaboration with biologists from New York State Department of Environmental Conservation, Vermont Cooperative Fish and Wildlife Research Unit, and the University of Vermont. The colonies on both Little Galloo Island and Long Island had been actively managed to control cormorant populations since 1999 and 1998, respectively, mainly through egg oiling and nest control (Farquhar et al. 2000, 2003; Coleman 2009, Chapter 2). We trapped adult cormorants on their nests using padded leg-hold traps (King et al. 1998) at the Oneida Lake and Lake Ontario sites, and captured adult cormorants at night with large landing nets at the breeding colonies on

2 of the Four Brothers Islands in Lake Champlain. In addition to recording weights and morphometric measurements on all captured birds, we also collected blood samples for molecular sex determination through a commercial lab. Adults trapped on Little Galloo Island were captured on nests that had been oiled, but we were not able to monitor their nesting behavior after the initial deployment. On Oneida Lake, cormorants were trapped on both oiled and and un-oiled nests. The nesting history of cormorants caught on Lake Champlain was unknown, but they were collected at a site that had not been subjected to nest management (Duerr 2007).

TDR and release mechanism

Because the double-crested cormorant is an extremely wary and unpredictable species, it is very difficult to recapture specific individuals in the late summer. Thus, we incorporated a programmable releasing mechanism into the tag design to allow for the recovery of the data archiving TDR tags (Coleman et al. 2008). We staggered the duration of tag deployment at each site based on weekly increments (i.e., 2, 4, 6, 7, or 8 weeks) to guard against loss of all tags through site abandonment. The actual release from the birds was programmed to occur at night, when cormorants are usually found roosting on land. The TDRs transmitted unique VHF radio signals, allowing for identification and tracking of individual birds, and for the location and recovery of the tags once released. Dates of deployment were influenced by availability of the component parts of the tags, and by the schedules of cooperators at 2 of the sites.

The TDR "tag" was composed of 2 main elements: an electronic time-depth recorder (Advanced Telemetry Systems, Isanti, Minnesota, USA) and the programmable release device (Alpha Omega Computer Systems, Corvallis, Oregon, USA). The manufacturer calibrated the TDRs in a pressure chamber prior to deployment and again after recovery to verify accuracy to ± 0.3 m. A subset of TDRs (n = 9) were also field tested by timed submersion to known depths in Oneida Lake to

verify consistency between units. The TDRs sampled ambient pressure every 2 seconds, thus dive times and water depths were recorded at 2 sec intervals, resulting in a maximum error in dive durations of <4 sec. The release device was designed to position the TDR on the dorsum of a bird, backpack-style, using a Teflon® ribbon harness (Dunstan 1972, King et al. 2000). The release device was integrated with the harness, and served as a platform for the attachment of the TDR. In 2002 we tested encapsulation materials to reduce the weight of the release device, resulting in 2 different models: cast epoxy ($\overline{x}$ = 27 g) and conformal coating ($\overline{x}$ = 19 g). Since both models were based on the same circuit board, they had approximately the same dimensions: 63 x 21 x 15 mm. A TDR weighing approximately 33 g was attached to each platform with silicon adhesive, for a total weight of approximately 61 g and 53 g respectively (≤3% mean body weight after selecting for larger individuals). A 3 mm thick neoprene pad was glued to the bottom of each release device to cushion the birds' backs. The tag assembly was designed to be streamlined and not positively buoyant so as not to hinder diving activity. The conformal coating failed in 2002 due to water incursion, resulting in the premature release of all tags deployed on Oneida Lake, so we abandoned that encapsulation method for 2003. Molds for encapsulating release devices were improved in 2003 to reduce weight ($\overline{x}$ = 24 g), resulting in a mean tag weight of 59 g.

Analysis

We used Raven sound analysis software (v. 1.2.1, Cornell Laboratory of Ornithology, Ithaca, New York, USA) to analyze the dive profile data retrieved from the TDRs. The program Rhythm was used to convert the dive profile data to a file format compliant with Raven, to quantify dive duration from initiation and completion times, and to report maximum depths reached per dive (see Cooper and Mills 2005).

We manually verified every dive identified by Rhythm and used the waveform interface of Raven to augment the data tables with any unidentified dives.

We used the MIXED procedure in SAS (v. 9.1.3, SAS Institute Inc., Cary, North Carolina, USA) to perform repeated measures ANOVA to test if daily foraging effort, expressed as the total amount of time cormorants spent diving per day, differed at each of the three colony locations, and to test if diving depth was affected by daily or seasonal constraints. Julian day was used as a seasonal measure, and we categorized daily dive activity in relation to the earliest sunrise and latest sunset for both years and all 3 locations. Therefore, the hours between 05:11 and 10:59 were considered morning, 11:00 to 13:29 was midday, 13:30 to 20:47 was afternoon, and 20:48 to 05:10 was night. Because we used the minimum sunrise and maximum sunset times, much of the twilight, or crepuscular, period is included in the morning and afternoon categories, however, given the long time-span of tag deployment, there were many days where the nighttime category includes a significant amount of pre-dawn and post-dusk twilight conditions. Also, data from the 1st day of deployment, and a few of the 2nd days depending on the time of capture, were omitted to allow time for the birds to acclimate to the harness and tag assembly.

RESULTS

We obtained dive profile data for 22 individual cormorants: 9 from Oneida Lake, 8 from Lake Ontario, and 5 from Lake Champlain. When compiled, the data represent foraging activity over 520 days, resulting in 491 full days after the first days of deployment and any partial last days are removed. Over those 491 full days, the TDRs recorded 87,900 dives, roughly half of which were from Lake Champlain and 1/3 from Lake Ontario. Technical and mechanical problems arose each year with several of the tags deployed at Oneida Lake, resulting in a much lower recovery rate

and shorter deployment durations than expected for that colony, but successful returns from both Lake Ontario and Lake Champlain exceeded our expectations. The duration of deployment over all sites ranged from 3 to 55 days (Table 5.1), and spanned periods of incubation, nestling and fledgling care, and post fledging (although individual nesting behavior was not documented). Consistent long-term data were recovered for cormorants on Lake Ontario and Lake Champlain, with over 3 weeks of foraging activity recorded for 4 and 5 individuals per colony, respectively. Given the earlier deployment at Lake Ontario, there is less chronological overlap between data from Lake Ontario and those collected at the other 2 sites (Fig. 5.1.), however, when both years are combined, there is a period from late June through late July in which we have data from all 3 lakes. Because we mostly selected larger individuals, tags were deployed on more male cormorants than female, and Oneida Lake was the only location where we recovered data from female birds (n = 5).

Timing of daily dive activity

The timing of daily dive activity was similar at all three locations, but patterns were not identical. A clearly bimodal activity pattern was evident for cormorants foraging on Oneida Lake and Lake Champlain, with peak activity recorded at approximately 10:00 and 16:00 (Fig. 5.2). Diving effort at Lake Ontario was more generalized, especially in the morning hours, but did appear to build through the day and peak at around 16:30. The main foraging effort also began earlier in the morning at Lake Ontario than at the other sites, with several dives recorded before the earliest recorded time of sunrise, approximately 05:21 for eastern Lake Ontario during that period (Fig. 5.2). Little Galloo Island was also the location with the most nocturnal activity, mainly due to the predawn dives, but a number of dives were also recorded in the hours following sunset. A total of 935 dives were recorded for Lake Ontario cormorants between 20:48 to 05:10 (the hours delineating nighttime as defined above),

Table 5.1. Deployment duration, average number of dives per day, and physical attributes for double-crested cormorants fitted with time-depth recorders on three lakes in the northeast U.S. Mean values are ± 1 standard deviation

Lake	Bird	Weight (kg)	Wing length (mm)	Sex	Date deployed (mm/dd/yy)	No. days	No. dives	Mean no. dives day^{-1}	Max. depth (m)	Mean depth (m)	Mean dive time day^{-1} (min)
Ontario	LO12	2.20	330	male	05/28/02	14	2,959	227.6 ± 80.6	22.1	6.3 ± 3.8	89.1 ± 23.3
Ontario	LO13	2.30	335	male	05/28/02	36	2,791	82.1 ± 50.7	18.3	5.8 ± 2.9	38.6 ± 25.1
Ontario	LO14	2.20	334	male	05/28/02	14	1,814	139.5 ± 71.9	22.7	7.4 ± 4.3	62.9 ± 27.7
Ontario	LO16	2.20	333	male	05/28/02	10	1,376	172.0 ± 107.5	8.7	3.4 ± 1.0	54.3 ± 29.9
Ontario	LO17	2.20	321	male	05/28/02	54	6,787	174.9 ± 88.9	25.8	6.7 ± 3.9	77.3 ± 35.1
Ontario	LO20	2.15	333	male	05/28/02	28	4,519	167.4 ± 105.2	18.9	4.8 ± 3.3	62.9 ± 30.9
Ontario	LO21	2.15	324	male	05/28/02	28	6,162	236.7 ± 126	19.1	3.7 ± 2.1	63.7 ± 31.1
Ontario	LO26	2.05	325	male	05/28/02	18	2,605	161.8 ± 81.8	17.7	5.5 ± 2.9	52.5 ± 22.5
Oneida	OL04	1.75	302	female	06/29/02	7	322	80.5 ± 51.7	10.6	2.5 ± 1.8	26.6 ± 15.5
Oneida	OL06	2.05	316	male	06/29/02	8	712	147.0 ± 118.9	12.1	4.6 ± 1.8	89.1 ± 57.0
Oneida	OL35	2.20	318	male	06/24/03	3	220	110.0 ± 49.5	15.3	10.6 ± 3.8	66.8 ± 35.7
Oneida	OL11	1.95	295	female	07/17/03	6	1,074	268.5 ± 38.1	9.9	3.5 ± 1.3	97.2 ± 9.7
Oneida	OL37	2.30	321	male	07/22/03	15	2,769	213.0 ± 115.8	15.5	6.5 ± 4.6	98.3 ± 68.9
Oneida	OL38	1.75	308	female	07/22/03	36	7,869	224.8 ± 82.2	14.3	4.7 ± 1.8	72.0 ± 24.2
Oneida	OL39	1.85	305	female	07/23/03	10	881	97.9 ± 78.8	13.9	5.0 ± 2.3	34.9 ± 27.9
Oneida	OL40	1.90	315	male	07/23/03	11	232	25.8 ± 18.8	4.8	2.5 ± 1.0	8.1 ± 6.4
Oneida	OL43	2.00	311	female	07/23/03	8	1,021	145.9 ± 70.9	7.8	2.3 ± 1.1	46.4 ± 25.7
Champlain	LC1	1.95	334	male	07/03/03	24	6,068	263.8 ± 114.9	7.8	2.3 ± 1.4	95.4 ± 41.1
Champlain	LC2	2.00	328	male	07/03/03	46	12,338	274.2 ± 93.6	8.5	2.2 ± 1.2	103.9 ± 37.9
Champlain	LC3	2.05	340	male	07/03/03	55	9,622	181.5 ± 97.7	8.0	1.6 ± 1.0	62.0 ± 29.4
Champlain	LC4	1.95	338	male	07/03/03	43	7,349	179.2 ± 97.9	8.6	2.5 ± 1.4	66.3 ± 31.6
Champlain	LC6	2.05	325	male	07/03/03	55	8,410	158.7 ± 79.7	8.2	2.3 ± 0.9	57.2 ± 28.2

Figure 5.1. Duty chronology for time-depth recorders deployed on double-crested cormorants trapped on breeding colonies at 3 prominent sites in New York. Tags deployed on Lake Ontario (2002), Lake Champlain (2003), and Oneida Lake (2002) were all activated on the same day (specific to each lake), thus the vertical lines depicting termination dates for the individual tags are also indicative of the duration of deployment. Tag deployment on Oneida Lake in 2003 was a more active process, and cormorants were trapped over several different days, so bar length in 2003 is not indicative of the duration of active duty.

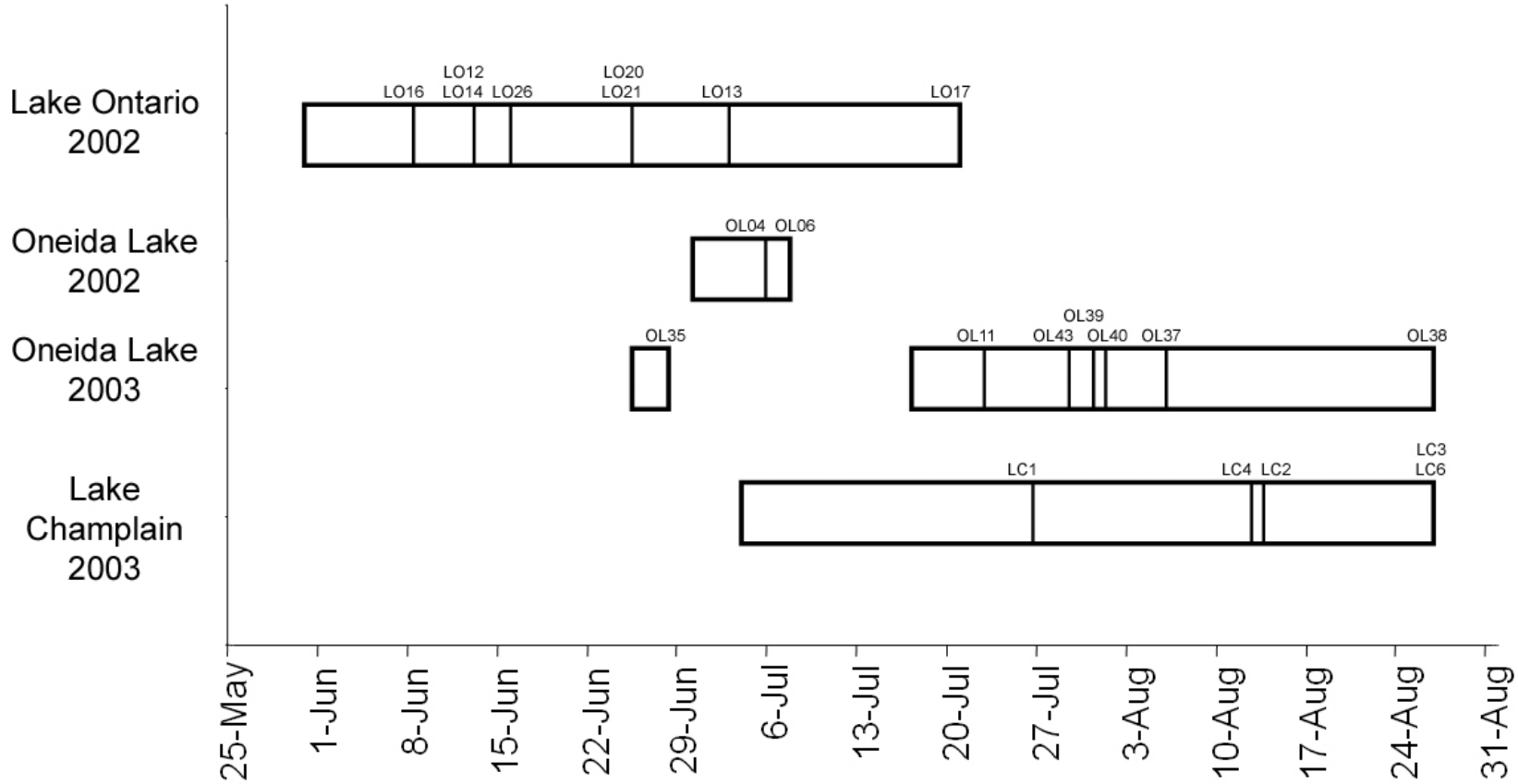
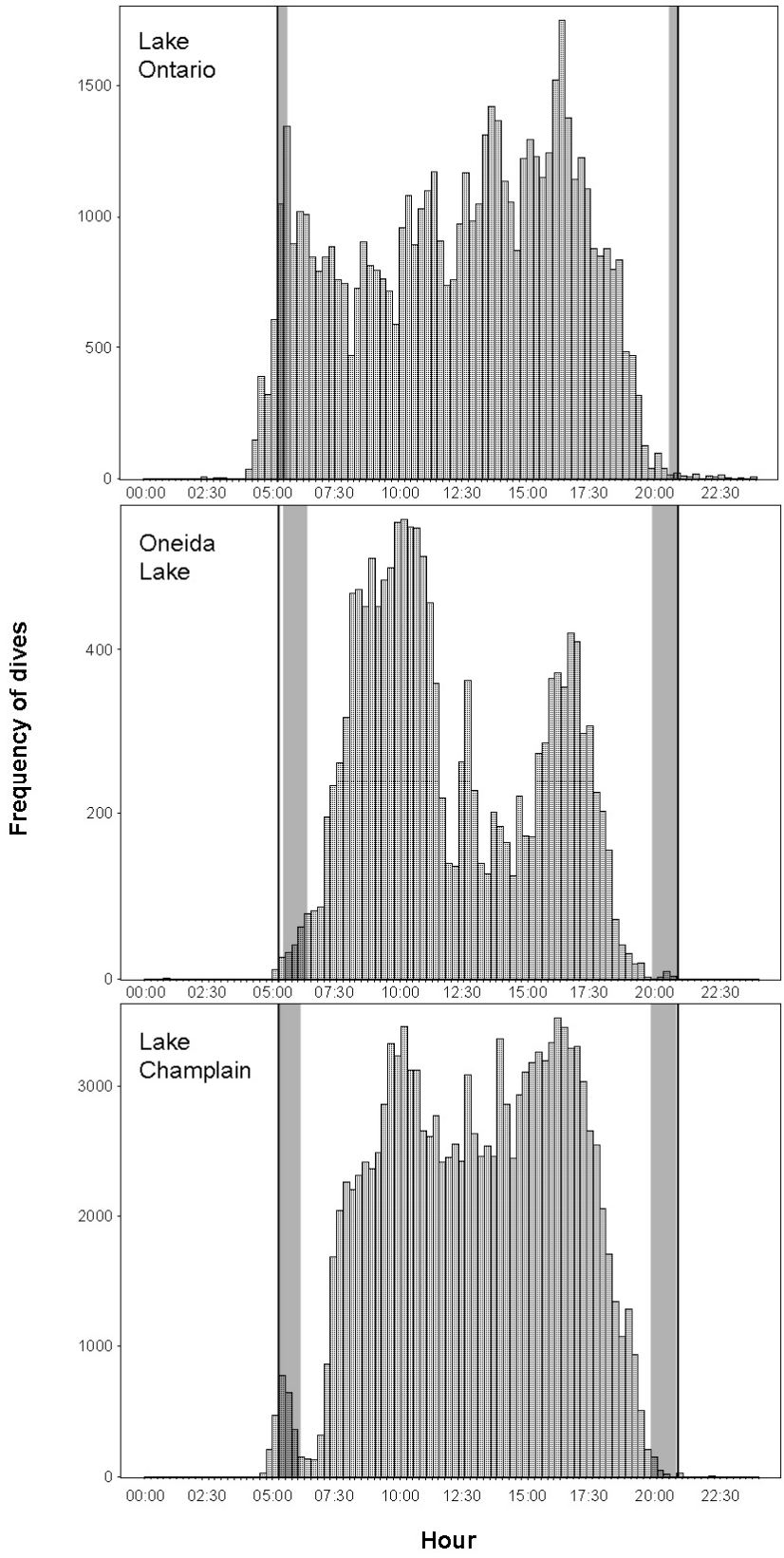

Lake Ontario
2002
LO16
LO12
LO14
LO26
LO20
LO21
LO13
LO17
Oneida Lake
2002
OL04
OL06
Oneida Lake
2003
OL35
OL39
OL11
OL43
OL40
OL37
OL38
Lake
Champlain
2003
LC1
LC4
LC2
LC3
LC6
25-May
1-Jun
8-Jun
15-Jun
22-Jun
29-Jun
6-Jul
13-Jul
20-Jul
27-Jul
3-Aug
10-Aug
17-Aug
24-Aug
31-Aug

Figure 5.2. The cumulative number of dives recorded for double-crested cormorants at each of three different lakes in New York. Histogram bars represent the number of individual dives performed within 15 min. blocks, relative to the time of dive initiation on a 24 hour scale. Data for Lake Ontario were collected from 8 different cormorants, spanning the dates: 28 May - 23 July, 2002. Data for Lake Champlain were collected from 5 different cormorants, spanning the dates: 3 July - 25 August, 2003. Data for Oneida Lake were collected from 9 different cormorants, spanning the dates: 29 June – 7 July, 2002, and 24 June – 27 August, 2003. The thin black lines represent the time of the earliest sunrise (05:11) and the latest sunset (20:47) at all three locations. Width of solid gray bars indicates the range of sunrise and sunset for the different locations: Lake Ontario (05:20-05:41 and 20:35-20:47), Oneida Lake (05:27-06:22 and 19:49-20:47), and Lake Champlain (05:11-06:07 and 19:45-20:43). Time of day is presented in Eastern daylight saving time (GMT – 4 hours).


Lake
Ontario
1500
1000
500
0
00:00
02:30
05:00
07:30
10:00
12:30
15:00
17:30
20:00
22:30
Oneida
Lake
400
200
0
Lake
Champlain
3000
2000
1000
Frequency of dives
Hour

representing 3.2% of the total number of dives logged for that colony. In contrast, only 38 (0.25%) and 323 (0.74%) dives were detected over that same time period at Oneida Lake and Lake Champlain, respectively.

Dive frequency and daily duration

The daily number of dives made by foraging cormorants, and the total amount of time that cormorants were engaged in diving, varied by day and by bird (Table 5.1). However, repeated measures ANOVA did not reveal a significant effect of location (lake) on the number of dives conducted per day ($F_{2,82} = 0.55$, $P = 0.58$) or the total amount of time that cormorants spent diving per day at the different sites ($F_{2,84} = 0.98$, $P = 0.38$). Moreover, mean and median total dive time for all individuals was approximately 1 hour at all three lakes, with a range of daily diving activity spanning 1 to 246 minutes (Fig. 5.3, Table 5.2). Julian day had a significant effect on total diving time ($F_{1,156} = 5.28$, $P = 0.02$), but no time trend is apparent. There was no significant interaction between Julian day and either sex or lake.

Dive depth

The depths to which cormorants dove also varied considerably by individual and by day, and also by lake (Fig. 5.4, Table 5.1). Cormorants on Oneida Lake and Lake Ontario frequently dove to 10 – 15 m, but the birds on Lake Champlain never exceeded 8.6 m. In fact, the majority of dives at Lake Champlain did not exceed 2 meters depth, but the tags from the other lakes indicate a fairly wide range of dive depths (Fig. 5.5). The deepest dive recorded was from Lake Ontario, and was part of a pelagic dive sequence. However, the 25.8 m dive was twice as deep as the dives that immediately preceded it, suggesting the active pursuit of a specific prey item (Fig. 5.6). Despite the apparent differences in depth utilization, location only approached significance when individual effects were controlled through repeated measures ANOVA ($F_{2,15} = 2.81$, $P = 0.09$). The physical characteristics of individual birds were

not found to significantly predict diving depth across all 3 lakes ($F_{1,15} = 0.39$, $P = 0.54$; $F_{1,15} = 2.29$, $P = 0.15$; $F_{1,15} = 0.00$, $P = 0.95$ for sex, body weight, and wing length, respectively).

As we found with dive time, Julian day did have a significant effect on maximum dive depths ($F_{1,87000} = 899$, $P < 0.0001$), and cormorants at Lake Ontario and Lake Champlain displayed trends towards deeper dives over the duration of TDR deployment. The time of day also significantly affected diving depth ($F_{3,87000} = 270$, $P < 0.0001$), with the largest deviations from mean depths occurring at night (Fig. 5.7). Cormorants on Lake Ontario and Oneida Lake generally dove less deeply between sunset and sunrise, and both mean and median dive depths were lower at night than during the daylight periods. Conversely, nighttime dives on Lake Champlain were generally deeper than those conducted during the day, but the mean depth of those dives (3.5 m) was comparable to those recorded at the other lakes (3.7 m at Oneida Lake and 4.0 m at Lake Ontario). Lastly, dive duration was positively correlated with depth as revealed by partial correlation, controlling for the effect of lake ($r = 0.56$, $P < 0.0001$). Mean individual dive durations ranged between 17 and 34 sec, and the overall mean duration was 22 sec (Fig. 5.8, Table 5.2).

DISCUSSION

Tag effects

Any time a tag or marker is attached to an animal, the propensity exists to alter behavior and/or performance, and possibly survival. The TDR/release assembly we deployed on cormorants was heavier than the VHF transmitters that have frequently been used for this species (e.g., Stapanian et al. 2002, Anderson et al. 2004, Coleman et al. 2005, Duerr 2007), and was slightly heavier than the 45 g satellite transmitters

Table 5.2. Daily diving activity of double-crested cormorants at three lakes as recorded by electronic time-depth recorders

Lake	No. full days of diving activity for all birds	Mean individual dive time day^{-1} ± SD (min)	Median dive time day^{-1} bird^{-1} (min)	Minimum dive time day^{-1} bird^{-1} (min)	Maximum dive time day^{-1} bird^{-1} (min)	Mean dive duration ± SD (sec)
Oneida Lake	86	64.0 ± 43.8	61.9	0.9	245.7*	21.8 ± 13.0
Lake Ontario	189	62.3 ± 31.4	58.8	1.0	159.1	22.4 ± 11.0
Lake Champlain	216	70.4 ± 37.9	64.6	3.0	198.4	21.8 ± 8.4
Combined	491	66.2 ± 36.8	61.7	0.9	245.7*	22.0 ± 10.2

* The second highest time day^{-1} for Oneida Lake was 180.5 min

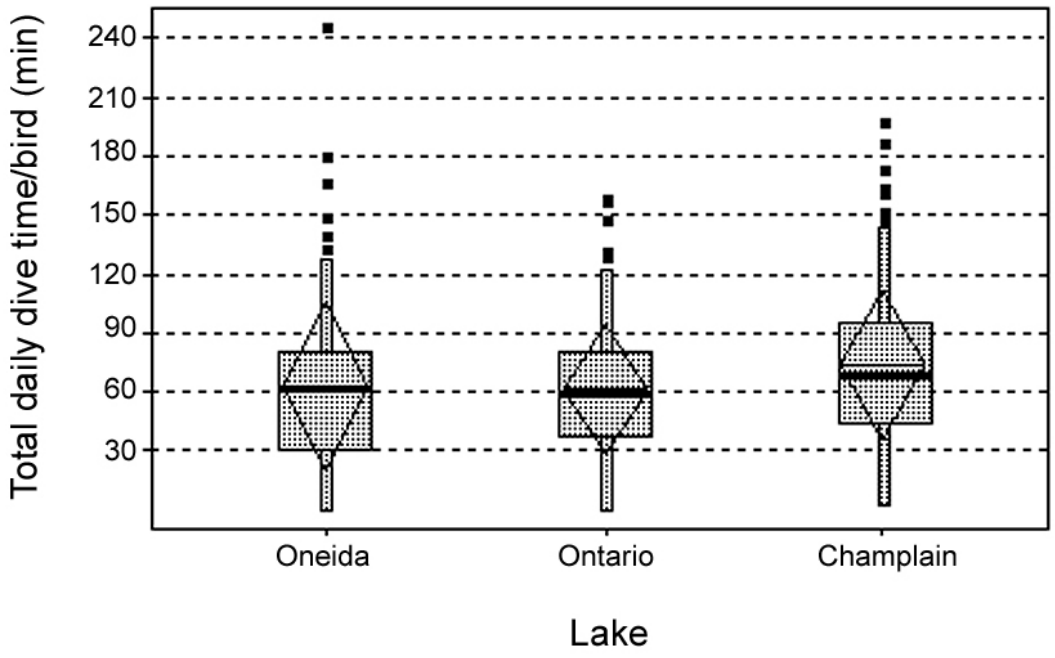


Figure 5.3. Box and whisker plot for the total daily dive time per individual cormorant at three New York lakes. Heavy black lines in the box represent median values. The diamond shapes depict mean dive time per day, with the pointed ends on top and bottom depicting 1 SD from the mean.

Figure 5.4. Box and whisker plot representing the maximum depths reached in all dives recorded for double-crested cormorants at three New York lakes. Heavy black lines bisecting the box represent median values. Cormorants are clustered by lake, OL = Oneida Lake, LO = Lake Ontario, and LC = Lake Champlain. See Table 5.1 for individual sample sizes

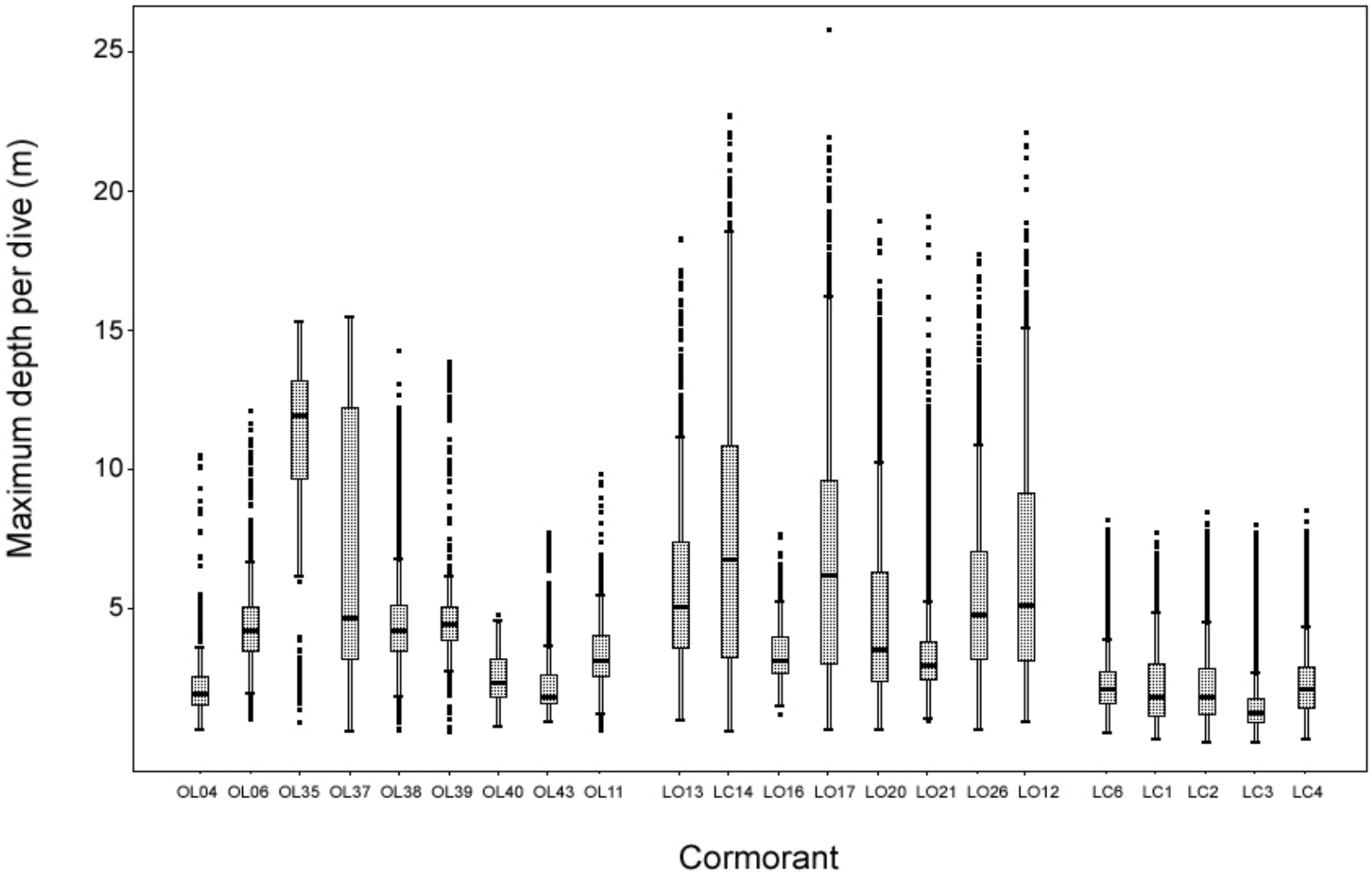
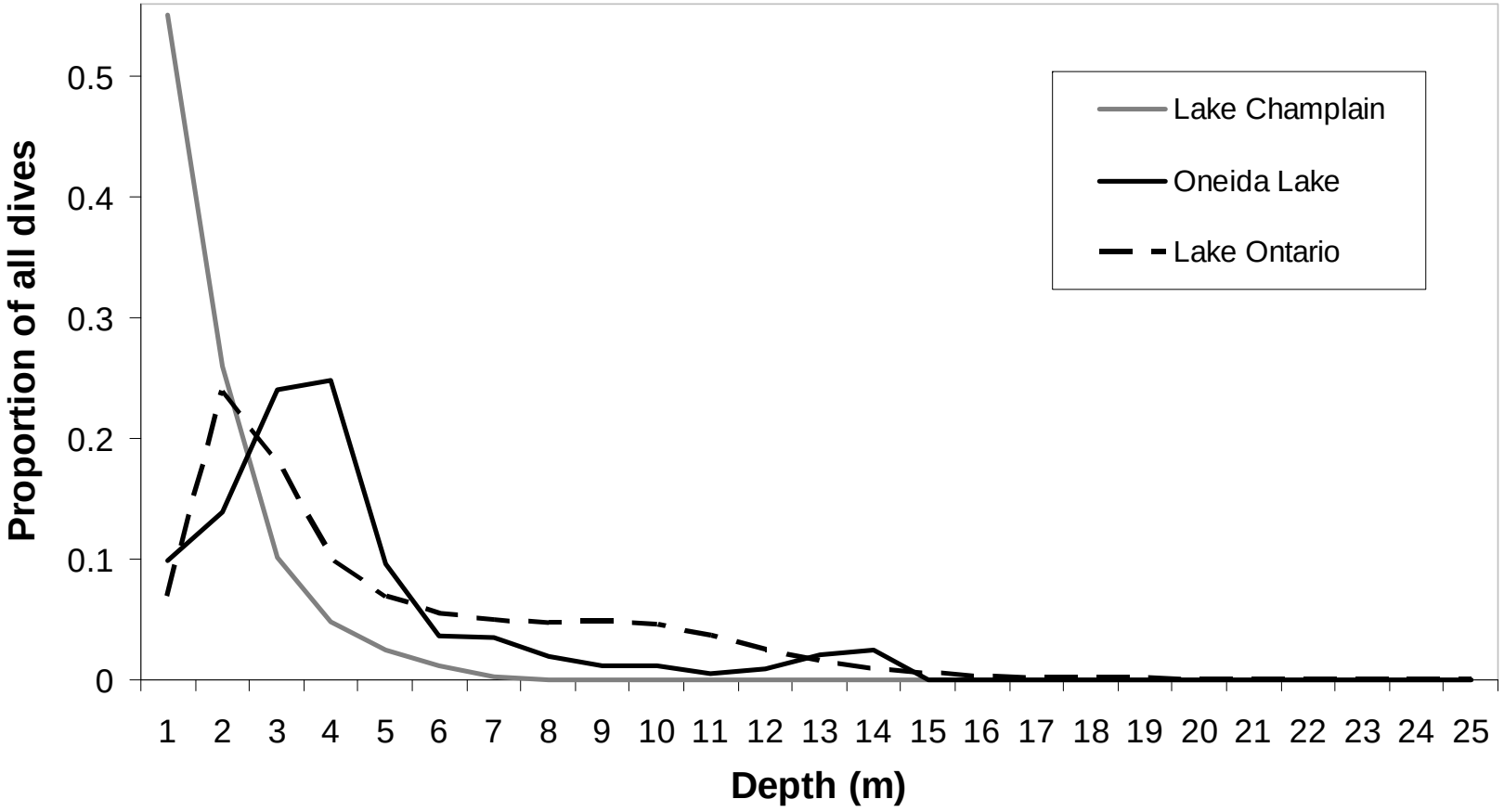
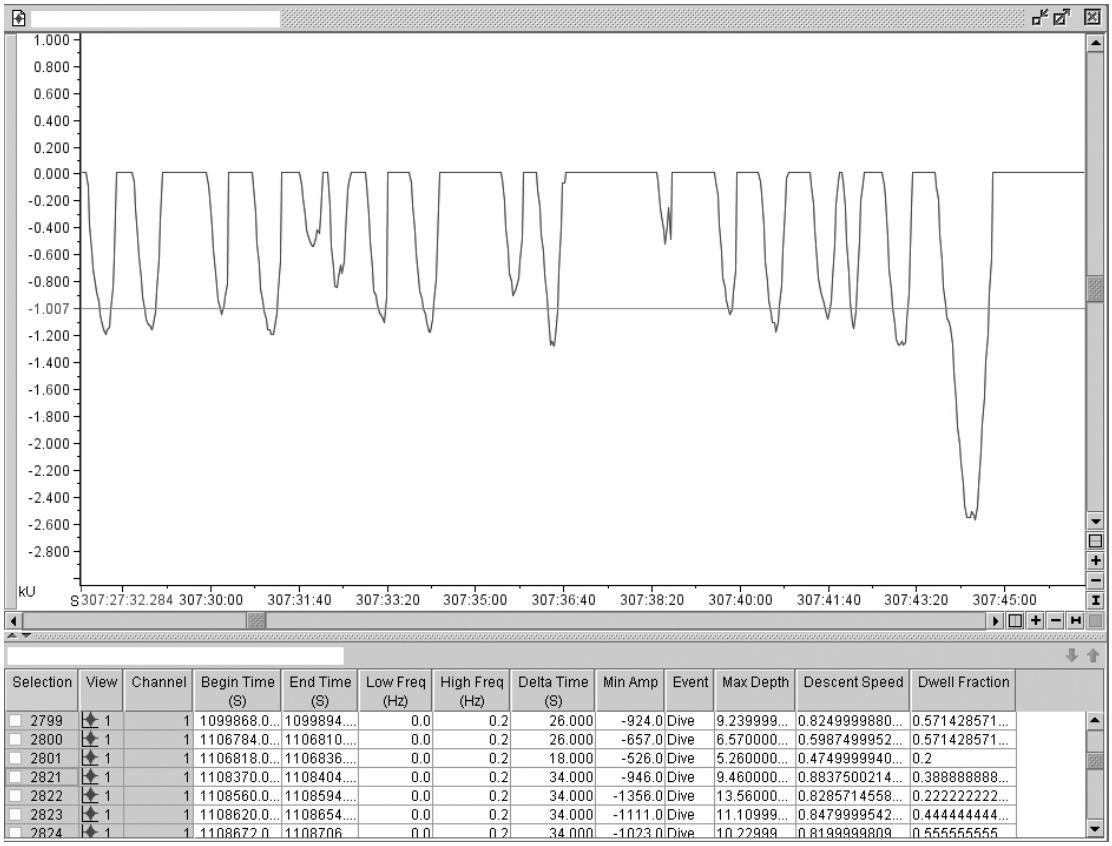

Maximum depth per dive (m)
25
20
15
10
5
OL04
OL06
OL35
OL37
OL38
OL39
OL40
OL43
OL11
LO13
LC14
LO16
LO17
LO20
LO21
LO26
LO12
LC6
LC1
LC2
LC3
LC4
Cormorant

Figure 5.5. Maximum depths of foraging dives, by proportion of all dives per lake, for double-crested cormorants studied on Oneida Lake, Lake Ontario, and Lake Champlain, USA.


Proportion of all dives
0.5
0.4
0.3
0.2
0.1
0
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24 25
Depth (m)
Lake Champlain
Oneida Lake
Lake Ontario



Selection	View	Channel	Begin Time (S)	End Time (S)	Low Freq (Hz)	High Freq (Hz)	Delta Time (S)	Min Amp	Event	Max Depth	Descent Speed	Dwell Fraction
2799	1	1	1099868.0...	1099894....	0.0	0.2	26.000	-924.0	Dive	9.239999...	0.8249999880...	0.571428571...
2800	1	1	1106784.0...	1106810....	0.0	0.2	26.000	-657.0	Dive	6.570000...	0.5987499952...	0.571428571...
2801	1	1	1106818.0...	1106836....	0.0	0.2	18.000	-526.0	Dive	5.260000...	0.4749999940...	0.2
2821	1	1	1108370.0...	1108404....	0.0	0.2	34.000	-946.0	Dive	9.460000...	0.8837500214...	0.388888888...
2822	1	1	1108560.0...	1108594....	0.0	0.2	34.000	-1356.0	Dive	13.56000...	0.8285714558...	0.222222222...
2823	1	1	1108620.0...	1108654....	0.0	0.2	34.000	-1111.0	Dive	11.10999...	0.8479999542...	0.444444444...
2824	1	1	1108672.0	1108706	0.0	0.2	34.000	-1023.0	Dive	10.22999	0.8199999809	0.555555555

Figure 5.6. Dive profile for a double-crested cormorant foraging on Lake Ontario in July, 2002. The profile depicts a pelagic dive sequence, consisting of V-shaped dives, and shows the deepest dive recorded for any cormorant in this study (25.8 m). The figure also depicts the waveform interface and selection table of the bioacoustics software Raven (v. 1.2.1, Cornell Laboratory of Ornithology, Ithaca, New York, USA). The horizontal line labeled "-1.007" represents 10.07 m depth.

Figure 5.7. Box and whisker plot describing maximum depths per dive for individual double-crested cormorant at three New York lakes, grouped by time of day. Morning hours are 05:11 - 10:59, Midday is 11:00 - 13:29, Afternoon is 13:30 - 20:47, and Night is 20:48 - 05:10. The heavy black lines bisecting the boxes represent median values, and the diamond shapes depict mean dive time per day, with the pointed ends on top and bottom depicting 1 SD from the mean.

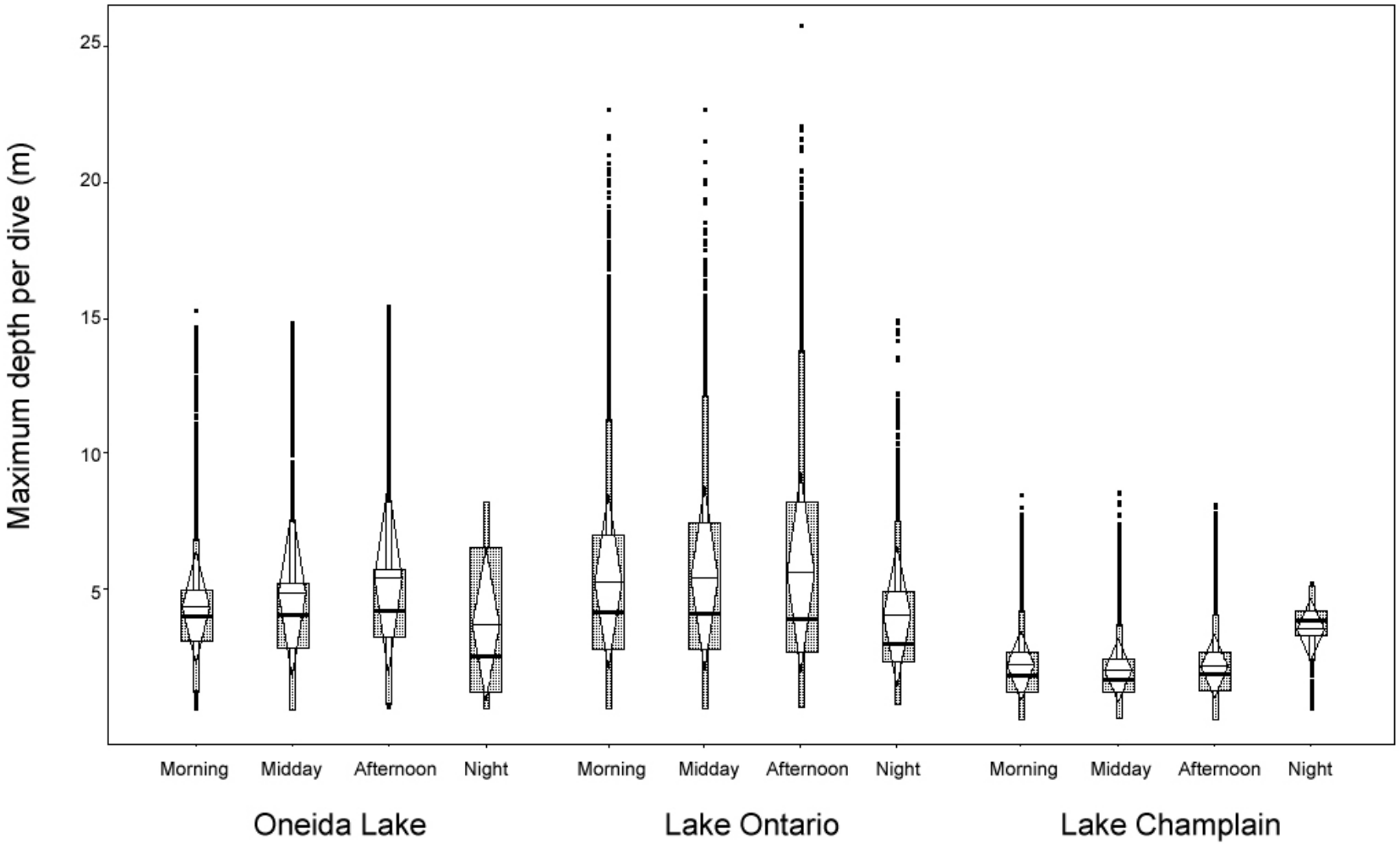

Maximum depth per dive (m)
25
20
15
10
5
Morning
Midday
Afternoon
Night
Morning
Midday
Afternoon
Night
Morning
Midday
Afternoon
Night
Oneida Lake
Lake Ontario
Lake Champlain

Figure 5.8. Mean individual dive durations (± 1 SD) for double-crested cormorants from 3 lakes in New York. Cormorants are clustered by lake, OL = Oneida Lake, LO = Lake Ontario, and LC = Lake Champlain. See Table 5.1 for individual sample sizes.

Mean individual dive duration (sec)
40
35
30
25
20
15
10
5
0
OL06
OL04
OL43
OL39
OL11
OL35
OL40
OL37
OL38
LO16
LO12
LO21
LO13
LO14
LO20
LO26
LO17
LC4
LC3
LC6
LC2
LC1
Cormorant

that had previously been successfully deployed on cormorants from the same region (see Werner et al. 2001). To minimize the effects of tag weight, we purposefully selected heavier individuals, generally ≥ 1.95 kg, but did include some lighter individuals from Oneida Lake in order to study differences by sex (male double-crested cormorants are larger than females, Johnsgard 1993). However, studies of similarly sized congeneric cormorants have demonstrated the ability of these diving birds to manage electronic tags with even greater weights without evident impairment, albeit with shorter deployment duration (Croxall et al. 1991 (72 g), Grémillet et al. 2006 (240 g), Watanuki et al. 2008 (72 g)). While we were not able to assess the physical condition of our study animals after the tags had released, the fact that all birds in this study also carried colored leg bands allowed many of the cormorants to be re-sighted in subsequent seasons, suggesting a low impact of TDR deployment on bird survival (personal observations; Bird Banding Laboratory, Patuxent Wildlife Research Center; personal communication: D. Capen, A. Duerr, D. T. King, I. Mazzocchi, and D. V. C. Weseloh). Therefore, while we cannot refute the possibility that the weight and/or drag associated with the TDR tags may have impacted the energetic cost of foraging within study individuals, we are confident that the behavioral data we present here are representative of the adult cormorant populations residing on the three lakes we studied.

Dive depth

This study is the first to use TDRs to examine the underwater behavior of free-ranging double-crested cormorants. The data we retrieved from the TDRs correspond with those from previous observational studies of dive duration, and with postulations about the diving capabilities of this species based on diet samples and associated water depth (Mendall 1936, Ross 1974, Palmer 1962, Cooper 1986). One of the earliest such accounts was provided by Lewis (1929), who reported an observation from

Quebec of a diving cormorant surfacing with a sculpin, a demersal fish, in water approx. 22 m deep. This 80 year-old observation is consistent with our recorded maximum dive depths from Lake Ontario. In general, however, previous accounts report the majority of cormorant foraging activity to take place in water ≤9-10 m deep (Lewis 1929, Custer and Bunck 1992, Harper 1993, Neuman et al. 1997, Stapanian et al. 2002, Coleman et al. 2005), which is further corroborated by the depth data we recovered (Figs. 5.4 and 5.5). No dives exceeded 9 m in Lake Champlain, and in Oneida Lake and Lake Ontario, only 7.3 % and 14.5% of dives exceeded 10 m, respectively.

The maximum dive depths we report here are not as great as those reported for congeneric species. Dive depth and duration are associated with body mass, due largely to a differential capacity to store oxygen (Butler and Jones 1997, Enstipp et al. 2001), and this factor has been implicated in intra- and interspecific differences in diving performance in cormorant species (Cooper 1986; Croxall et al. 1991; Wanless et al. 1991, 1995; Watanuki et al. 1996). The cormorants in our study are similar in size to many of those described in the literature, so it is likely that the maximum depths we observed did not represent the fullest capability of the double-crested cormorant. Most likely, the diving behaviors we observed were merely those necessary to forage effectively in Lake Ontario.

Energetic expenses generally increase with depth for diving cormorants due mostly to heat loss through the reduced efficiency of their already thin fat layer, the compression of insulative air trapped in plumage with increasing pressure, and the high thermal conductivity of water, which is colder at depth (Wilson and Wilson 1995; Grémillet and Wilson 1999; Enstipp et al. 2001, 2005). However, compression of trapped air at greater depth also reduces the positive buoyancy that birds making shallow dives must continually overcome to remain submerged, especially early in the

foraging bout, before feathers become saturated and less capable of holding air. Thus, there are energetic costs associated with both shallow and deep dives that exceed the mere act of swimming, and the relative expense of these dives, in this context, requires further examination. Despite the energetic concerns and the obvious differences in depth utilization at the three lakes, once the individual effect of individual bird was controlled, location was not found to have a significant effect on either the number of dives conducted per day or the total time spent actively diving each day at the three locations. This was unexpected given the considerable behavioral, biotic, and abiotic differences between the colony sites. Oneida Lake is a shallow polymictic lake that remains warm through much of the summer months, while Lake Ontario and Lake Champlain are deep cold-water lakes with pronounced thermal stratification. The resident cormorant population is relatively small on Oneida Lake, resulting in less potential for intraspecific competition than at the other sites. The lake is managed for yellow perch (*Perca flavescens*) and walleye (*Sander vitreus*), which constitute the majority of cormorant diets sampled over 10 years (VanDeValk et al. 2002; Rudstam et al. 2004; Coleman 2009, Chapter 3). The mean distance to foraging locations on Oneida Lake was less than 3 km in 1999 and 2000 (Coleman et al. 2005), and the foraging locations we recorded during this study (unpublished data) did not reveal a deviation in spatial distribution from that of previous work. In contrast, the other colonies we studied had much larger cormorant populations, with over 4700 nesting pairs on Little Galloo Island in 2002, and almost 3000 pairs on the Four Brothers Islands in 2003 (Weseloh et al. 2002, Duerr 2007), and nesting islands surrounded by deep colder waters. Forage fish populations in the open waters near the nesting islands have been found to be dominated by alewife (*Alosa pseudoharengus*) in Lake Ontario and rainbow smelt (*Osmerus mordax*) in Lake Champlain (Rand et al. 1994, Pientka and Parrish 2002, Parker-Stetter et al. 2006), and these species constitute a

considerable portion of cormorant diet at these locations (Ross and Johnson 1995, Fowle 1997, Neuman et al. 1997, Ross et al. 2002, Johnson et al. 2003, Duerr 2007). Foraging distances measured at these colonies have been considerably greater than at Oneida Lake, averaging 13 km at Lake Ontario and 15-21 km at Four Brothers in Lake Champlain (Harper 1993, Neuman et al. 1997, Duerr 2007). The combination of longer flight distances and colder water temperatures suggest greater energetic costs for cormorants on the 2 larger lakes than on Oneida Lake, but this was not reflected in a reduced foraging effort on Oneida Lake. It may be that differences in energy expenditure are offset by the better quality of pelagic forage fish consumed at these sites, since both alewife and rainbow smelt have been found to have greater energy densities than many of the common littoral prey species (Rand et al. 1994). However, this is unlikely since cormorants also consume a fair amount of yellow perch and sunfish (*Lepomis* spp.) at these sites as well (Burnett et al. 2002, Johnson et al. 2003, Duerr 2007), more akin to the diet of cormorants on Oneida Lake.

Timing of daily dive activity

Patterns in the timing of daily foraging effort, as revealed by diving activity, were not consistent across the three lakes. Previous research on daily foraging habits at Oneida Lake revealed a bi-modal pattern of activity in radio-tagged birds, with roughly equal numbers of birds foraging during morning and afternoon hours in mid-summer (July), but with efforts skewed towards greater activity in morning hours by late summer (August) (Coleman and Richmond 2007). This same pattern was revealed by the dive data for birds tagged on Oneida Lake in this study, many of which were tracked during late summer which corresponds with Period 2 from Coleman and Richmond (2007) (Fig. 5.2). However, morning and afternoon dive activity were more evenly distributed at Lake Champlain than on Oneida Lake, with a relatively large amount of effort exhibited through midday. Lastly, diving activity on

Lake Ontario did not reveal the strongly bimodal pattern demonstrated at the other sites, and also by congeneric cormorant species at different locations (see review in Coleman and Richmond 2007). The cormorants tagged on Lake Ontario began their foraging bouts earlier in the day than birds on the other lakes, often in the pre-dawn twilight hours (Fig. 5.2). After an initial peak effort in early morning, diving activity of Lake Ontario cormorants increased steadily through the day to ultimately peak in late afternoon. There are two potential explanations for the differences in the timing of foraging effort we observed. One possibility is that the birds on Lake Ontario were in the incubation stage in June, 2002, albeit with oiled eggs, and perhaps the periodic change of nest attendance will tend to expand the window of time in which adult cormorants forage in a day, or perhaps the individuals left tending nests in the previous afternoon had a more urgent need to feed in the morning. This scenario does not necessarily account for the pre-dawn initiation of foraging activity, however, and is not as plausible an explanation as one that associates cormorant behavior with that of a prey species. Cormorants breeding on Little Galloo Island feed heavily on alewife, which constituted 86% of the total diet by number in June – July, 2002 (Johnson et al. 2003) the same period as our study. Alewife are pelagic epilimnetic planktivores during both day and night in Lake Ontario (Olson et al. 1988) but may move to shallower water at night to feed on zooplankton (Boscarino et al. in review). It is possible that cormorants in Lake Ontario forage in the pre-dawn twilight hours to take advantage of alewife that are at shallower depths than later in the day. This hypothesis is supported by twilight and nighttime dives recorded for Lake Ontario being mostly V-shaped pelagic dives, and they are less deep compared to daytime dives (Fig. 5.7). Alternatively, shallow dives under twilight or nighttime conditions may be a response to reduced light levels compared to daytime conditions. Lacking relevant diet data for pre-dawn dives, this hypothesis is unsubstantiated. However,

such foraging behavior does warrant further study as it could reveal yet another level of behavioral complexity in food-web dynamics and interspecific interactions in the Great Lakes, and may also be indicative of a complex temporal awareness in cormorants.

Lastly, it is worth noting that the flexibility that cormorants demonstrate in their foraging habits provide them with the adaptability to capitalize on changes to prey populations on a seasonal and annual basis. Doubtless, this adaptability has enabled cormorant populations to grow as rapidly as they have in recent years. Were this study to be replicated in 2008, we would likely see differences in foraging behavior in response to changing prey assemblages in the lakes we studied. Since 2002 the exotic round goby (*Apollonia melanstomus*), a benthic species, has rapidly pervaded all of Lake Ontario and has quickly become a prominent prey species for cormorants at colonies around the region (Somers et al. 2003, Ross et al. 2004, Coleman et al. *in review*). Similarly, alewife (*Alosa pseudoharengus*) was first discovered at the northern end of Lake Champlain in 2003 (Vermont Fish and Wildlife Department 2005), and is expected to become well established as a major forage species within the lake (Good and Cargnelli 2004). If, or when, that occurs, cormorants foraging on Lake Chaplain will likely adapt their diving behavior to accommodate the distributions of this familiar invader.

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